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Causes and Significance of Morphological Variation in Fishes

GEORGE W. BARLOW

Introduction

MANY ICHTHYOLOGISTS have tended to assume extreme positions as to whether observed differences between populations of a given species of fish are caused by genetic differences or merely by dissimilarities of environments. Early workers were inclined to regard differences, especially countable ones, as indicative of genetic divergence alone. Many of these forms were formally recognized as subspecies, or species (examples are cited in Jensen, 1944). The weight of thought swung the opposite direction after the discovery that characters could be altered through manipulation of the environment. Now ichthyologists commonly assume differences between populations of a species are environmentally induced unless a genetic basis can be demonstrated experimentally. The bulk of recent literature, however, is concerned primarily with the elucidation of the effect of environment on a given genetic stock. The problem of genetic divergence between populations of a fish species, or within a single population, has not received as much attention and evidence along these lines, therefore, is meager (but see Gordon, 1957).

It is essential to the progress of systematic ichthyology, as well as to the planning of experiments on this problem, that the nature of morphological variation in fishes be properly understood. Since the early papers by Hubbs, only Tåning (1952) has reviewed this subject. Tåning stressed the role of the environment in determining meristic characters, and also fostered the misleading notion of *day-degrees*.

The primary objective of the article at hand is to put forth arguments to support what is meant to be a more balanced point of view. Morphological clines, especially for those forms which have somewhat disjunct populations, are regarded as the consequences of environmental modifications coupled with adaptive genetic changes. In the course of writing the article it also became necessary to reconsider the problem of the production of variation in fishes, particularly, meristic variation.[1] As a result, a refinement of Hubbs's (1926) hypothesis has been developed to account for the genesis of meristic variation in the hope it may give direction to the design of future experiments.

Variation in Size and Shape

Variation in size and shape of fishes will not be treated as fully as meristic variation. More is known about meristic variation, so it is profitable to treat that subject in greater detail. Nonetheless, a synopsis of what is known about genetic and environmental factors in the control of size and shape of fishes should assist the reader in evaluating the major thesis of this article.

Differences in size and shape are apparent in comparisons between fish from waters of different temperatures. Almost invariably the more northern representatives of a species, or of a genus, are larger than those to the south (Hubbs, 1926;

[1] The term meristic variation is used here in the widest sense, referring to all countable characters, though most of the discussion centers on variation in the number of fin rays and vertebrae.

Vladykov, 1934). The changes in body proportions have not been as thoroughly investigated as those in segmental structures, but some tentative generalizations can be made. Northern, slowly growing races of a species usually have smaller heads, eyes, maxillaries, and fins than do their southern counterparts, although opposite effects are not uncommon (Hubbs, 1926; Vladykov, 1934; Martin, 1949; and included references).

Growth rate apparently determines body shape by altering the timing of transition from one growth stanza to another (Huxley, 1932; Martin, 1949). Each growth stanza is recognized by a characteristic relative growth of the body part. The transition from one stanza to the next is usually abrupt and produces a new relationship between the growth of the part and the body as a whole. If the logarithms of the part, and of the length of the fish are plotted, a straight line is obtained for a given stanza. The transition to the next stanza is revealed by an inflection of the slope of the line. Differences in the relative sizes of body parts between fish of the same species are the results of changes in the timing of the inflections, not of the slopes of the lines. Because of this, growth changes in early life are particularly efficacious in modifying the form of the fish (Martin, 1949). Changes in relative growth sometimes occur at sexual maturity, but seldom after.

Evidently, the environment can modify the shape of a fish (Vladykov, 1934; Svärdson, 1953, and earlier references therein; Williams, 1954) by acceleration or retardation of the rate of development (Hubbs, 1926; Martin, 1949). But the scope and direction of such variation that is due to genetic differences is not understood, and research is sorely needed here. Martin (1949) noted that within a group of rainbow trout, *Salmo gairdneri*, the fish with small heads were the ones that grew slowly. Presumably genetic differences were responsible for the divergence. However, the rainbow trout reared at high temperatures, consequently faster growing fish, had smaller heads than those developed at lower temperatures. Mortality was high in the warmest-water groups and may have been selective.

Other differences in shape are known that might seem at first to be the result of environmental irregularities, but more likely have a genetic cause. Some fluviatile fishes, particularly cyprinids, display morphological gradients that correspond to degree of adaptation to moving waters (Hubbs, 1941). The forms that inhabit rivers with strong currents are more streamlined; they are terete and have longer, more falcate fins. "Individual populations living in aberrant ecological conditions retain the proper forms, thus showing that these form characteristics are inherited" (Hubbs, 1941). Similar racial differences in morphology, but related to nutritional types, occur in the American poeciliids (especially *Mollienisia sphenops*); breeding experiments have shown that the differences are hereditary (Hubbs, 1941).

Meristic Variation

The relationship between latitudinal distribution of fish and the number of elements in serially repeated characters gave rise to one of the first and most widely applicable generalizations of ichthyology. Time and again it has been shown that the number of such elements is progressively greater to the north (Hubbs, 1926; Vladykov, 1934; Tåning, 1952; and references therein). Most exceptions have been associated with special local conditions such as colder water currents to the south (Jensen, 1944), differences in altitude in fresh-water systems (Bailey and Gosline, 1955), relatively constant temperature springs (Miller, 1948; Weisel, 1955), differences in time of spawning (Bailey and Gosline, 1955), or salinity gradients (Schmidt, 1917). Sometimes the cline is reversed for one fin only, so that the number of elements in that fin is higher in more southern parts of the distribution

of the species; the other meristic characters, however, show the expected increase from south to north (Hubbs, 1921, 1926; Schultz, 1927). In the Southern Hemisphere the few cases that have been studied show that the counts increase from north to south, that is, in the opposite direction to that observed in the Northern Hemisphere (Hubbs, 1926; Vladykov, 1934); this increase is related to the reversed temperature gradient. In both the Northern and Southern Hemispheres there is a good correlation between cooler environmental temperatures and higher meristic numbers.

Apparently the number of serial elements is determined by developmental rate (Hubbs, 1926; Gabriel, 1944; and references therein). Longer developmental periods usually produce higher counts in meristic structures. This then is the mode of action of lower temperatures since developmental rate varies directly with temperature. Other agents which retard development, such as high salinities and low oxygen tensions, have effects parallel to those of low temperatures (Hubbs, 1926; Tåning, 1952; Seymour, 1956).

Furthermore, those characters which are last to appear during ontogeny are the most labile. The last-formed epidermal plates on the side of the three-spined stickleback, *Gasterosteus aculeatus*, are the ones lacking in seminude races (Roth, 1920). Caudal vertebrae vary more than abdominal vertebrae (Hubbs, 1922); apparently the caudal vertebrae develop last (Ford, 1933), but this is not certain (Blaxter, 1957). The nape is the last region to be scaled in many fishes, and in certain races of these species it is the commonly naked region (Hubbs, 1926). Fin rays are added, or lost, at the posterior edge of the fin, but not always (Barlow, 1958), and these are the last to appear during development (Hubbs and Hubbs, 1945; Gosline, 1947; Lindsey, 1954).

The number of fin and vertebral elements are determined during a relatively short span of time during early development. Tåning (1952) called this the "sensitive" period. Some determination of the counts occurs before this period, but to a much smaller degree. The sensitive period transpires before hatching in salmonid fishes (Tåning, 1952; Seymour, 1956), and in *Fundulus heteroclitus*, the killifish (Gabriel, 1944); however, the sensitive period falls several days after hatching in *Macropodus opercularis*, the paradise fish (Lindsey, 1954), and in *Pleuronectes platessa*, the plaice (Molander and Molander-Swedmark, 1957); this may also be the case in *Clupea harengus*, a herring (Hempel, 1953; Blaxter, 1957), and in *Gobius ruthensparri*, a goby (Heincke, 1880). The paradise fish has an extremely short incubation period (about two days), and the newly hatched larvae are incompletely developed by comparison with those of the first three groups mentioned above. In the plaice the sensitive period lies near the time of metamorphosis from the pelagic to the benthic stage of the life history. The sensitive period thus appears to be related to some developmental stage, independent of the presence of a protective egg membrane.

The sensitive periods of different structures do not coincide. It is known for *Salmo trutta*, the sea trout (Tåning, 1952), and the plaice (Molander and Molander-Swedmark, 1957) that the vertebrae are determined earlier in development than the fin rays. Also the sensitive periods of the different fins are not the same in the sea trout; this was not investigated in the plaice. In the paradise fish, too, the abdominal vertebrae are fixed considerably earlier in development than are most of the other meristic characters. The number of fin elements is determined at about the same time as the caudal vertebrae (Lindsey, 1954).

Experiments involving only two temperatures, and these not precisely controlled, have demonstrated that the number of countable elements is greater in fish reared at the lower temperature, and

less in those reared at the higher temperature. In these comparisons fish of a relatively uniform genetic background were used. Johnny darters, *Etheostoma nigrum*, reared at the cooler temperature, had more vertebrae than their sibs from the higher temperature (Lagler, *in* Bailey and Gosline, 1955); each of the temperatures varied over about 2°C. during development. Higher counts of vertebrae and of scales were recorded from *Salmo kamloops* raised at the lower temperature (Mottley, 1934, 1937), but temperatures and oxygen tensions were not well controlled. Dannevig (1950) also found an inverse relationship between two developmental temperatures and the mean number of vertebrae; the temperatures fluctuated considerably. In each investigation the temperatures utilized were reasonably close to the expected temperatures for development under natural conditions.

Two investigators, Gabriel (1944) and Blaxter (1957), observed that vertebral counts of fish reared at several different temperatures were progressively higher in those from the lower temperatures. Gabriel raised killifish, *Fundulus heteroclitus*, at three different temperatures; the mean number of vertebrae was higher at the lower temperatures. Blaxter kept eggs of herring, *Clupea harengus*, at many different temperatures. He counted the myotomes of the herrings at two different developmental stages: at 50% of the embryos hatched, and at 50% with the yolk sac absorbed (myotome numbers were shown to parallel vertebral numbers). Myotome counts plotted versus developmental temperatures yielded a straight line with a negative slope, that is, higher counts at lower temperatures.

Contrary to expectations the number of elements in the dorsal fin of *Lebistes reticulatus*, the guppy, and the dorsal and anal fins of the plaice decrease at lower temperatures. In repeated experiments Schmidt (1919) compared guppies developed at 18°C. with those at 25°C.; fewer dorsal fin rays were formed in fish from 18°C. Observations in nature led Hubbs (1924) to conclude that parallel changes take place in the dorsal fins of two other viviparous cyprinodonts. Molander and Molander-Swedmark (1957) reared two different sets of sibling plaice at 6°C., 8°C., and 10°C. Far fewer elements were formed in the dorsal and anal fins at 6°C. than at 8°C. and 10°C. However, the vertebrae responded differently, and this will be considered below.

In some fishes temperature–induced changes do not follow a simple pattern of higher counts at low temperatures, and lower counts at high temperatures. For instance, in salmonid fishes (Schmidt, 1921; Tåning, 1952; Seymour, 1956; and perhaps Mottley, 1937), and in the plaice Molander and Molander-Swedmark, 1957), the mean vertebral number within a genetic stock was in each instance lowest at some intermediate temperature. Progressively higher counts were found at temperatures above and below this intermediate temperature (as in Fig. 1). Thus vertebral numbers plotted as a function of temperature yielded V-shaped curves. The response of the fins to temperature changes in salmonids was similar to that of the vertebrae but more complex. Invariably a V-shaped curve described the relationship between temperatures and counts. In Tåning's work on the sea trout, however, the V-curves for the dorsal and anal fins were inverted, and strongly asymmetrical. In the dorsal and pectoral fins the inflection of the curve was near the upper end of the temperatures employed, but near the lower end for the anal fin.

Lindsey (1954) found a similar V relationship between temperature and meristic numbers in the paradise fish. Vertebrae, basal elements of the dorsal fin, segmented rays of the anal fin, and pectoral fin rays were all minimal at the intermediate temperature. These counts were higher at the higher temperature as well as at the lower. On the other hand, the

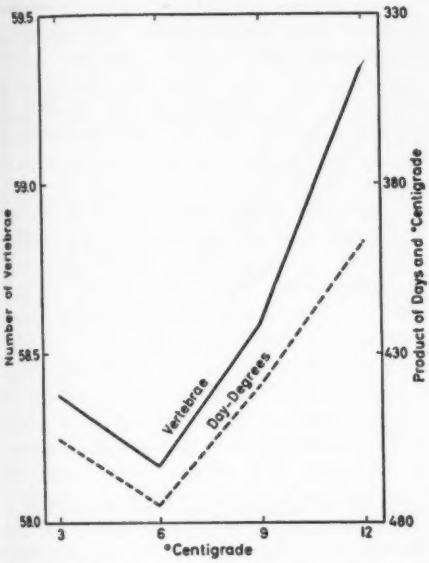

FIG. 1. The day-degree ordinate has been inverted to reveal the correspondence between the two curves, and to convey the notion of rate. The temperatures are those of the water in which the sea-trout embryos were incubated. The solid line shows the mean number of vertebrae for each temperature group. The broken line represents the products of the holding temperatures and the number of days to 50% of the eggs hatched. The figure is from Markmann (1954), except that Markmann labeled the day-degree curve as t, the "incubation period."

number of anal spines was progressively higher at the lower temperatures. The number of dorsal spines and also of soft dorsal rays was about the same at all temperatures.

Changes in the salt content of the developmental medium can alter the effect of temperature on meristic characters. Heuts (1949a) compared the differences induced by temperature and salinity in fin-ray numbers of the three-spined stickleback, *Gasterosteus aculeatus*. Two genetic stocks were utilized, one a fresh-water race, the other a brackish-water race. In one race, the salinity that caused the *maximum* variation in the median fins with temperature changes coincided with that salinity which produced the *minimum* variation in the other race, and vice versa. The greater variation in each group occurred at the salinity to which the particular race was best adapted. (It seems probable the restriction of the range of counts in non-adaptive media could have been the result of differential mortality; many fish died before the counts were taken.) Furthermore, when the embryos were reared in the salinities that caused maximum divergence, lower temperatures produced higher median fin counts in each race. At other salinities the relationships were repeatedly altered, and in no predictable fashion. In the pectoral fin the maximum divergences also occurred at the optimal salinities. At all salinities the pectoral fin counts taken from the fish of the fresh-water race were highest in those reared at an intermediate temperature. However, in the brackish-water race the pectoral fin was almost unaffected by changes in temperature at higher salinities.

The hypothesis that meristic characters are dependent on rate of development appears to be valid even in the light of the complex results reviewed in the foregoing. In the poeciliid *Xiphophorus maculatus* the interval between the birth of successive broods averages 31 days, and the modal number of caudal vertebrae is 15; in *X. helleri* the interval is eight days longer, and the mode of the caudal vertebrae is greater by two (Gordon and Benzer, 1945). In four genetically different stocks of chinook salmon, *Oncorhynchus tshawytscha,* the minimum number of vertebrae (but the greatest number of dorsal and anal fin rays) was obtained from fish developed at some intermediate temperature (Seymour, 1956). And the same intermediate temperatures brought about the maximal rate of embryonic growth. Among killifish eggs from a single pair of adults, and at a given temperature, the first fish to hatch had the lowest number of vertebrae (Gabriel, 1944). The fish that developed over a

longer span of time had progressively more vertebrae. In addition, the killifish that developed slowly were larger than those that hatched first. Similarly, in a newly hatched group of siblings of the plaice, *Pleuronectes platessa*, raised at the same temperature, the fish were increasingly larger at each higher vertebral count (Dannevig, 1950). It seems plausible the larger plaice had a longer developmental period than the smaller ones. Among nonsiblings of the plaice, however, no correlation between size and number of vertebrae was evident.

Markmann (1954), using Tåning's seatrout material, developed a unique hypothesis to account for variation in vertebral number. It behooves me to criticize his arguments because his hypothesis conflicts with the one presented below. Markmann purported to show that the number of vertebrae laid down by the embryo is directly proportional to the rate of development. The lowest number of vertebrae and the longest incubation period (slowest rate) are said to occur in the fish reared at the intermediate temperature of 6°C. (Fig. 1). The upper curve shows the number of vertebrae and the lower is said to portray the "incubation period"; the latter is plotted reciprocally to convey the notion of rate. But by the "incubation period" Markmann really means the *day-degrees* of incubation, which is the product of the actual incubation period in days and the particular temperature. The close correspondence between the two curves was assured in the calculations of the "incubation periods" by empirically assuming −0.5°C. as the "biological zero" instead of 0°C. I calculated the true, or absolute, incubation periods from Markmann's data, and found the rate of development actually increased steadily from the lowest to the highest temperature (Fig. 2). Furthermore, the Q_{10} decreases at each temperature, which means that the incubation period at 6°C. really shows the greatest decrease (increase of rate) relative to the developmental rate at 3°C.

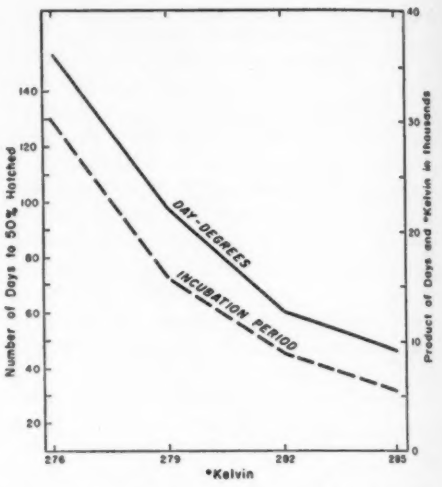

FIG. 2. This figure has been derived from Figure 1, and data in Markmann (1954). For the day-degrees products, °Kelvin have been used instead of °Celsius. The incubation period is the actual number of days to 50% of the eggs hatched.

Then I formed a new day-degree product using the Kelvin temperature scale instead of the Celsius scale. This has the advantage of avoiding the arithmetical difficulties that arise as the numbers approach zero. This time the relationship between actual incubation period and temperature was preserved (Fig. 2). Undoubtedly the apex obtained by Markmann is an arithmetical artifact. There is no point in further criticism except to note that Markmann's hypothesis rests primarily on the presumption, derived from this artifact, that metabolism is lowest at the intermediate temperature of 6°C. This is also unlikely on purely physiological grounds because 6°C. is near the thermal optimum for development in this species. Markmann showed, for instance, that the sea trout reared at 6°C. achieved the greatest weight.

Heuts (1949a) has criticized the original hypothesis of Hubbs that developmental rates determine the number of meristic elements. The results he obtained with

sticklebacks raised at different temperatures seemed to him to be incompatible with this hypothesis. The first criticism was that the lengths of the embryonic lives of two genetically different races of sticklebacks were the same, although meristic characters were different. However, Heuts has not determined the sensitive period (Tåning, 1952) for the characters involved. This period need not occur before hatching (Lindsey, 1954). Without considering this, he transferred the fish of both races to fresh water right after hatching for further development. If, as he proved for the eggs, fresh water imposes a selective stress on the different races, then modification of the meristic characters conceivably still could be operating after the transfer. Further, mortality was appreciable before and after hatching and certainly could have been selective. As Heuts (1947) has pointed out, there is a strong correlation between morphological characters and degree of adaptation to different salinities in these fishes. And beyond these arguments the races are genetically different; the *relationship* between growth rate and differentiation of parts could be inherently dissimilar and hence produce different counts even though the two groups have equally long embryonic periods. Hubbs's contention that developmental rate determines the number of elements formed was clearly intended for those cases where a given genetic system is under consideration.

The second criticism put forth by Heuts (1949a) was that changes in salinity at a given temperature did not influence the developmental rates, but did modify the number of elements produced. It can be seen (Heuts, 1947a) that the percentage of eggs that survive to hatching is clearly different, depending on the salt content of the developmental medium. Once more, differential mortality is a serious objection. And so is the immediate transfer of the fish to fresh water upon hatching. In all fairness to the splendid work done by Heuts, the problem of differential, probably selective, mortality is the greatest difficulty to overcome in this type of experiment. Certainly differential mortality has not been obviated in most investigations of this problem. Only Tåning has had success in this respect.

Developmental rates are thought by Hubbs (1926) and Gabriel (1944) to determine meristic characters through the control of two different aspects of developmental physiology, to wit, growth and differentiation. In this scheme low temperatures retard growth more than differentiation. When the growth is slowed, the presumptive tissues presumably develop into a greater number of elements before the segments are fixed; conversely, rapid growth does not permit the differentiation of as many elements.

A model for the interaction between growth and differentiation can be envisioned along slightly different lines. Conceivably each structure has, in differing degrees, its own particular sensitivity. The differentiation of these structures may be more or less interrelated, as indicated by parallel changes in the median fins and vertebrae in some fishes. When the number of elements increases at lower temperatures, the differentiation of the structure is assumed to be less sensitive to the environment, not more, than is overall growth. As an example, let the differentiation of the vertebrae have a low temperature coefficient (Q_{10} or μ) and the growth of the embryo a high coefficient. Then growth will be retarded by low temperatures, but the rate of formation of vertebrae will be less diminished. Hence the vertebrae will form over a *relatively* longer period of time and more of them will be laid down. On the other hand, those characters which decrease in numbers at low temperatures, such as the dorsal fin rays in the guppy, could be explained on the basis of their having higher sensitivities (higher Q_{10}) to the environment than has total development.

This model would allow for the

V-shaped curves obtained by Tåning (1952) where the apex of the V falls at different temperatures for different fins and the vertebrae. These curves would be interpreted as showing points of inflection of the temperature coefficients. Seen in this manner the curves are reminiscent of the complex interactions between activity optima of different enzymes within a given system. This argument could be developed in like fashion to take into account the effects of other growth retarding factors such as high salinity, low oxygen tension, and the amount and duration of light exposure.

This model has wide application in that it is compatible with observed reverse and V-shaped relationships; otherwise, it is clearly identifiable with the original argument advanced by Hubbs (1926). It should be made clear, too, that this is not an explanation of how the differences are actually brought about; it is only a model. It is also consistent with the results of experiments involving "temperature shocks" (Tåning, 1952), especially if thermal acclimation is taken into consideration.

If fish are transferred from one temperature to another *just before* the sensitive period, the meristic characters are greatly modified, far more so than if the fish had been reared continuously at the second temperature (Tåning, 1952; Lindsey, 1954; Molander and Molander-Swedmark, 1957). The most significant feature of these manipulations is that the direction of induced changes in counts is extremely consistent. The number of elements always is increased when the transfer is from a higher to a lower temperature, and consistently fewer elements form when the fish are transferred from the lower to the higher temperature. It is worth noting that it was exactly these workers who discovered the complex temperature/fin-count relationships in fishes reared at constant temperatures.

Apparently the embryo is acclimated (Bullock, 1955, has reviewed acclimation phenomena) to the first developmental temperature. Sudden transfer to water having a different temperature, higher or lower, must result in a metabolic response in excess of the normal or acclimated level. Subjected to the same thermal shock, the differentiation of the meristic characters evidently has a lower sensitivity. Consequently transfers to higher temperatures produce lower counts, to lower temperatures, higher counts. In every instance (Tåning, 1952; Lindsey 1954; Molander and Molander-Swedmark, 1957) the results agree with this explanation.

Under uniform developmental temperatures the relationship between the temperature coefficients of growth and of differentiation are variable (as in the complex responses in trout, stickleback, and paradise fish). On the other hand, when temperature changes occur during development the temperature coefficient of growth processes appears to be higher (more labile) than that of differentiation. Thus when temperatures oscillate, particularly if too fast to allow for acclimation, the expectation is that a decrease in temperature will increase meristic characters; an increase will decrease the counts. This may resolve some of the conflicts between observations taken in nature and those in laboratories. The experiments of Heuts (1949a), Tåning (1952), and Lindsey (1954) for example, showed that the relationship between temperature and different meristic characters is complex when the temperatures are rigidly constant. Yet observations on the stickleback and sea trout from nature revealed a gradient of decreasing counts from north to south, hence from cool to warm temperatures. It should almost go without saying that constant temperatures are not natural.

Lindsey (1958) has suggested the north-south clines may be induced by changes in the amount of light impinging on the eggs because this environmental parameter varies more regularly with latitude

than does water temperature. Increased intensity (McHugh, 1954) and increased duration (Lindsey, 1958) of light caused the development of a lower number of vertebrae in two unrelated species of fishes. However, in these experiments many of the embryos died and selective mortality again may have been involved. A further reservation lies in the nature of the material. Both species used in these experiments, the grunion, *Leuresthes tenuis,* and the kokanee, *Oncorhynchus nerka,* deposit their eggs below the surface of the substrate. As a result the eggs normally develop in total darkness. The metabolism of these embryos might be unusually susceptible to the effects of increased illumination. In the experiments by McHugh, the physiology of the developing fish may have been adversely affected by the total elimination of clues to daily (*circadian*) periodicity. Constant light and temperature conditions are known to be inimical to the physiology of certain organisms (Pittendrigh, *pers. comm.*). It is worth noting, too, that some clines run in directions other than north-south. Bailey and Gosline (1955) found for many percid fishes that the best trends for shifts in vertebral numbers ran southwest-northeast. Until more experiments are available the role of light in producing clines will have to remain an open question.

Up to this point the discussion has centered on variability induced in meristic characters of the phenotype, without regard to the genotype. A genetic determination of meristic characters has been demonstrated both within and between populations, or races. According to Hubbs (1955) the dorsal and anal fin ray numbers in the subspecies of the mosquito fish, *Gambusia affinis,* are determined by the action of a single gene; the validity of this assertion has been questioned by Gordon (1957). In all other instances the characters behave as though determined by a multifactor system; undoubtedly, this is the usual situation. The progeny of the killifish, *Fundulus heteroclitus,* with high vertebral numbers also have high counts, and likewise for those from killifish with low counts (Gabriel, 1944). In the same way, the number of dorsal fin rays of new-born guppies is high or low depending on the parentage (Schmidt, 1919; Svärdson, 1945). Hybrids between races of the same species commonly have intermediate numbers of elements (Heuts, 1949a; Svärdson, 1953; Hubbs, 1955). Successive generations of a race of *Zoarces viviparus* transferred to a new environment continued to be recognizable from the endemic population on the basis of different vertebral and median fin counts (Ege, 1942). Different races of species reared under comparable conditions have dissimilar meristic characters (Mottley, 1937; Heuts, 1947b, 1949a; Seymour, 1956).

There have been numerous studies on natural populations of fishes. Sometimes it has been shown through investigation of meristic characters that genetic differences exist between the populations in question. Since the literature is large and the results variable I will restrict my comments to my own research (Barlow, 1958). Within a given year-class of a gobiid fish, *Gillichthys mirabilis,* there is no correlation between the pectoral and median fin counts. Thus the number of elements in each set of fins is independently determined. However, in successive year-classes shifts in the means of pectoral fins are paralleled by shifts in the means of the median fins. Fish developed in cold years show increases in the average pectoral fin count as well as in the means of the median fin counts. Therefore, the environment evidently modifies the counts in the typical way. Yet from population to population the number of elements in the pectoral and median fins is significantly negatively correlated, and in a regular way. The pectoral fin cline runs in the opposite direction to that of the median fins. Furthermore, *mirabilis* transferred from San Diego to the Salton Sea, a saline desert lake on almost the same lati-

tude, showed a tremendous increase in the counts taken from all fins. Remarkably, the ratio of pectoral fin rays to median fin rays remained the same, showing that the mean relationship between fins was unaltered. Thus the meristic cline apparently corresponds to a genetic cline. Studies on the metabolic physiology of different populations support this contention.

The variance of a given fin, or of the vertebrae, may be a parameter of greater utility than the mean. Within a given population of *Gillichthys mirabilis* the change in means may show significant differences from year to year. The variance, however, remains the same. Also, northern populations of *mirabilis* manifest greater fin-ray-count variation than do the southern populations.

Then if genetic differences underlie the meristic dissimilarities which exist between populations, or races, a question immediately comes to mind: are these changes in fin ray counts adaptive? We can disregard for the moment the problem of whether it is the observed difference itself that has selective value.

The transplantation experiments of Ege (1942) constitute perhaps the best demonstration of selection for fish with a particular number of vertebrae. One race of *Zoarces viviparus*, with a low vertebral count, was introduced into the enclosed habitat of another race, with a high count. So many fish of the first race were introduced that they were the dominant form. The first few year-classes showed a rise in the mean number of vertebrae. Then the mean decreased in succeeding years. A pronounced reduction in the number of vertebrae took place between birth and the age of one year in each of the year-classes. The mean value per year-class decreased from one-half to one and one-quarter vertebrae. Ege realized this meant a change in the genotype between the young and the adults of the same year-class. The selection was for fish with the lower vertebral number.

Laboratory reared stocks of a given fish species show greater variability than do the naturally occurring populations. Fin counts of laboratory reared cottids, *Clinocottus recalvus*, have a much greater range than do their natural counterparts (Morris and Scheer, 1957). Gabriel (1944) noted that even though he could experimentally produce high or low vertebral numbers in *Fundulus heteroclitus*, the count in the wild population was usually less variable than that in the laboratory. The vertebral mode of the wild population of *F. heteroclitus* was 32; the range was four. In the experimental fish the range was as low as four in one experiment but ran up to six and eight in the others. This is more striking with the realization that, in contrast to the fish from nature, each laboratory sample consisted of siblings reared at a uniform temperature and salinity. This implies the extremes had been present in the natural population but were eliminated, as would be predicted if the populations were genetically homeostatic (Lerner, 1954). From studies of specimens collected from nature Bailey and Gosline (1955) concluded that natural selection reduces the variability of vertebral numbers in a percid fish.

It is difficult to believe that the addition or subtraction of a few elements would materially affect the probability of the survival of a fish, though this may be the case. However, it is difficult to prove, or disprove, such a thesis.

The more profitable, but indirect, attack on this problem is to determine whether or not there is a correlation between meristic characters and obviously adaptive physiological processes. In the carp, *Cyprinus* (sp.?), certain genotypes that are said to be more viable than others were recognized by the degree and pattern of squamation (Kirpichnikov, 1945). Golovinskaya (1940) reported a mutant gene in the carp that appears to have the pliotropic effect of reducing vitality while decreasing the number of fin rays, scales, and gill rakers.

In four different races of the chinook salmon, *Oncorhynchus tshawytscha*, the vertebral counts were clearly different when the fish were reared under the same conditions (Seymour, 1956). The divergence in vertebral counts due to genetic dissimilarities between the races was greater than that induced within the phenotypes. In each race the optimum temperature for development (fastest development, lowest mortality, fewest aberrant fish) was different. Thus in *Oncorhynchus* genetic differences connected with the determination of vertebral numbers were correlated with adaptive changes in thermal responses.

In the stickleback, *Gasterosteus aculeatus*, physiological characteristics are correlated with lateral shield numbers as well as with vertebral numbers (Heuts, 1947a). Adults of the race adapted to fresh water are smaller and have far fewer lateral shields and slightly more vertebrae than the adults of the brackish-water race (Heuts, 1947b). The physiological characteristic studied was successful embryonic development in waters maintained at various constant salinities and temperatures. The embryos of the brackish-water race were generally better adapted for development at higher salinities than were the embryos of the fresh-water race. The complex nature of the results, though, leaves the matter an open question. However, later experiments (Heuts, 1956) with a geographically different race yielded a similar type of variation and consequently increase the confidence in the earlier experiments. The fresh-water and brackish-water races are interfertile and cross matings are thought to take place in nature, though at a low frequency. Hybrids between the races are morphologically intermediate, but physiologically they are the same as the maternal race.

Hubbs (1928) recognized the possibly genetic nature of clines of meristic characters in fish species. He advanced the hypothesis that differences in counts between geographically separated populations are indications of adaptive changes. In an extension of the ideas of Baldwin (1896), Hubbs suggested that species new to an area would be altered by the environment, and that these differences, being associated with adaptive changes, would become genetically fixed. The evidence for genetic differences between races, and for the adaptive significance of such changes, has been cited above. I would not care to extend the argument that meristic clines are genetically determined to include all the meristic clines that have been described for sundry fishes. However, I think it highly probable that genetically reinforced differences exist in those species where the populations are somewhat isolated from one another. This would include fresh-water forms, species from marine bays, and the shore species of oceanic islands. Pelagic marine species on the other hand probably are as panmictic as could be expected within each oceanic system or subsystem.

Summary

Variation in shape of fishes is poorly understood, but in general retarded growth seems to cause small heads and associated parts, and short fins.

In the meristic characters, slow development is commonly associated with high numbers of elements, fast development with low numbers. Different factors in the environment, such as temperature, salinity, and oxygen, may control the rate of development. The number of elements is determined during a short "sensitive" period in the embryonic, or larval, fish.

Plots of temperature during development versus number of elements formed, in precisely conducted experiments, have revealed a family of V-, or inverted V-shaped curves. However, changing the temperature just before the sensitive period always produced an increase in the counts when the temperature was lowered, and a decrease when the temperature was raised. The rate of differentia-

tion of each meristic character is thought to be more or less independent of the other meristic characters in its relationship to the overall growth of the embryo. Inflection points on the curves indicate reversals in the relationships. Disagreements in findings from the field and from the laboratory may be the result of monotonous, uniform conditions in the laboratory, an unnatural and possibly harmful situation. Experiments are needed which employ controlled, fluctuating parameters of the environment.

Genetic determination of variation in meristic characters has been demonstrated through typical breeding experiments, hybridization, and transplantation. It has also been deduced by comparing the nature of variation within a given year-class, between successive year-classes, and between populations.

The variation itself may be a more stable and useful indicator of genetic determinants than the mean.

Regular changes in counts, such as in geographical clines, probably reflect adaptive changes of a genetic nature.

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Recent Developments in Theoretical and Quantitative Taxonomy[1]

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THE LAST FEW YEARS have seen a revival of interest in taxonomy. Much of this has stemmed from what is often called experimental taxonomy or biosystematy, and the development of this field is well known. The purpose of this paper is to discuss some other recent developments in systematics. My own interest in taxonomy has come largely from problems in bacteriology, and in extenuation of this admission—for who indeed would ask a bacteriologist for wisdom on systematics!—I should perhaps say that bacteriologists are aware how bad their taxonomies are. This makes it easier for them to question assumptions which are far too readily taken for granted, and may help to liberate them from some of those clogging traditions, uncritically accepted, to which other biologists often seem obliged to pay lip-service. Some of these assumptions are re-examined here, together with their implications for the taxonomy of the future.

The Philosophy of Taxonomy

The philosophy of taxonomy—that is its methodology and basic ideas—is one of the most neglected fields in biology. This is due in part to the tendency for students to learn first a smattering of elementary general biology and then to study advanced special biology. Some parts of advanced general biology, such as evolutionary theory, are well taught, yet taxonomic theory, also advanced general biology, is generally neglected. Elementary taxonomy is commonly taught deplorably, while advanced taxonomy is ignored. The general feeling that evolution is dynamic and taxonomy is static has further tended to reduce interest in the latter. Yet taxonomy is the foot rule with which we measure both static taxonomic similarity and evolutionary change, and it is a surprising fact that we have given no real attention to the properties required of such a foot rule. It is indeed only recently that this deficiency has been realized.

The Epistemological Approach. All the recent advances in this branch of systematics seem to stem, either directly or indirectly, from a new approach which is epistemological, or, in plain language, which asks what information is required and contained in taxonomic systems. The pioneer in this field is J. S. L. Gilmour of Cambridge University, whose short and very simple paper in 1937 is a landmark. This marks a step forward along a path which was first suggested by Adanson in 1757 and developed at greater length in 1763. Michel Adanson was a Frenchman of Scottish descent, and neither the French nor the Scots (who are usually exceedingly prompt in acclaiming the celebrities of their own nation) nor biologists in general have given him the credit he deserves. His fundamental idea, which after nearly 200 years is now pervading taxonomy, is the postulate that *in creating a natural taxonomy every feature of the organism has equal weight.* The significance of this postulate is that it is equal weighting which yields the kind of classification which we recognize as being 'natural.' Adanson was the first to try to explain in any detail the real reasons why

[1] Based on a university lecture given on 9th February, 1959, at the University of Kansas, Lawrence, Kansas.

we group organisms into taxa in the manner we do (intuitively if not consciously). His somewhat ill-expressed arguments were rejected by his contemporaries, on precisely this point of equal weighting, and the massive influence of de Jussieu, de Candolle and Cuvier was thrown against him (e.g., de Candolle, 1813). They in turn built up natural classifications which, although they did not realize it, were in fact largely based on Adanson's principle. The point which Adanson made was that if you divide up your specimens, using in turn different parts or organs, and thus produce a large number of classifications each based on a different character complex, you will find that some of these classifications give almost the same end-result as others. This is because some characters are highly correlated with other characters and it is plain that whenever we separate two sharply defined groups we must rely on such a correlation. If we did not have such correlation between features, then of course we could not recognize the groups as distinct ones, since all the intermediate combinations of features would give rise to a network of intermediate forms of organism which no one would consider were all distinct taxa. This idea was not new, though Adanson expressed it more clearly than most; what was new was that he rejected any attempt to decide which characters were *a priori* most important, and based his natural classifications upon the correlations themselves, which in effect treated every character as of equal taxonomic importance. Those who are interested in Adanson's distinctive contribution should read the lucid exposition by Cain (1959a). Adanson's earliest work on this seems to have been on mollusks (Adanson, 1757).

The contribution of Gilmour (1937, 1940, 1951) was based on different premises, but it also implied the principle of equal weighting. He asserted that our concepts of taxa, to which we give taxonomic names, are generalizations based on large numbers of features, and that their value in taxonomy is directly related to the amount of information which they imply—what may be called their "content of information." Thus the name "mammal" and the concept *mammal* imply a large number of properties which are possessed by almost every individual belonging to this group. The concept *creatures which are black* is taxonomically trivial, since this implies only one property—blackness. Gilmour argued that natural classifications were nothing more than arrangements which brought together those creatures with the greatest number of common attributes. And neither "content of information" nor "greatest number of attributes" has anything to do with the idea of "importance of attribute" (Sneath, 1957a)—they are simply measures of the number of statements which can be made about the organisms. In fact I believe that the only satisfactory definition of a unit feature is that it is an attribute of an organism about which a single statement can be made conveying one unit of information (Sneath, 1957b). In the language of information theory it is 'one bit' of information, and this definition is applied, in one form or another (e.g., Cain, 1954:147), in all the quantitative taxonomic methods discussed later. Our estimate of the degree of overall similarity between two organisms (or, more strictly, between comparable stages of their life cycles), which is what we use to group them into taxa, is therefore a function of the proportion of features common to both organisms, and this is primarily what we mean by taxonomic affinity or closeness. Methods of measuring this overall similarity in quantitative terms are now being devised and are discussed in a later section. Like any statistical estimate overall similarity must be based on a sample of many features if it is to mean anything significant.

My own work with bacteria led me to this same position by another route, the consideration of just what taxonomic importance was and how it was to be meas-

ured (Sneath, 1957a). It is very clear that we all tend to overrate the importance of those features which we make our special interest. The morphologist emphasizes morphology, the physiologist physiology, and so on. This of course is only special pleading or lobbying, and really means "it is important to me because I am interested in it." And even granted that one feature is more important than another, it seems quite impossible to arrive at any rational way of giving an exact figure for their relative importance. Should ability to grow without oxygen be 10 or 11 or 100 times more important than the manner of locomotion, and why? If we cannot give a definite figure we can scarcely claim that taxonomy is a quantitative science. And it is of course quite fallacious to rely on the relative constancy of a feature in a group, since if we are setting out to create taxonomic groups we do not yet know what these groups are. Similar arguments apply to every class of feature, and we are therefore driven to assume that they must be all counted as equally important. Even the concept of a fundamental or basic feature is a logically unsound one, for if it means anything at all precise, it means that a lot of other features are found associated with it. Before we can prove this, we are just guessing; after proving it there is no need for the special weighting, since we can then simply include these associated features in our studies.

I should make it quite clear that I am using the phrase "importance in classification" in the restricted sense of "importance in creating taxonomic groups." We may legitimately consider some features as more important in *identifying* a specimen with an existing taxon, for here the word "important" means that this feature has in the past been found to be present in almost all the individuals of this taxon, and therefore it is likely to prove true of new specimens of this same taxon. This is what key-features really are: they are short cuts to accurate identification of new specimens when the taxa have already been well established—they are not features on which the taxa are based. For the latter purpose they must (1) be known and defined before the taxa are created, and (2) they must then be rigidly adhered to. They stand self-condemned on these counts, as a simple example will show: if a mammal is defined as a creature with mammary glands, then (1) there is no way satisfactory for taxonomy of rigorously defining a mammary gland before creating the taxon of mammals (for pigeons and tse-tse flies can be said to suckle their young) and (2) a mammal in which the mammae are missing is never placed in a new class outside the Mammalia.

Perhaps the most illuminating example of a natural taxonomy is one taken from a library. Every arrangement, whether of books or organisms, is artificial in the sense that it is made by man, and natural in the sense that it deals with real material objects, and one cannot say of an arrangement that it is true or false, or good or bad, unless one specifies the purpose at hand. If our taxonomics are the arrangements which we consider the *best* we must say what they are best for. The word *best* lies at the heart of taxonomic theory. A librarian can arrange books in many ways. If arranged alphabetically by authors, then it is only good for one purpose, which is to find it quickly if you know the author's name. It is quite useless as a guide to its size, color, or subject matter. It is a special arrangement for a special purpose, and the analogy in taxonomy is an arbitrary division on a single character, such as dividing higher vertebrates into four-legged and two-legged. Such divisions do not in general create the kind of entity we call natural taxonomic groups. But one can also arrange books in a *general arrangement*, by employing a summary of all their properties, and this leads to a classification which is predominantly by subject-matter since the printed statements in the book will greatly outnumber the other attri-

butes. This is the *best arrangement for general purposes,* because we will usually find what we want in the books of the appropriate subject, although we will never be certain to do so, and some books on borderline subjects will be difficult to arrange. This is therefore a general arrangement, best for general purposes, but *perfect* for none. Any intermediate situation can of course occur, and an arbitrary classification may be close to being a natural one because the taxonomist has intuitively selected for division of his organisms a character which does happen to give natural taxa. Orthodox taxonomy, what we loosely call "natural" classification, is precisely a general arrangement for general purposes (Sneath, 1958). Just as we could not claim that our library was a general arrangement if we considered chemical facts to be very much more important than any others (which would give a predominantly "chemical" arrangement), so we cannot claim that a taxonomy is a general one if we consider morphology or any other subject to be of overriding importance. Even a phyletic classification is a special classification, albeit a most useful one, which we may assume, *when we can get one,* to be close to a general classification.

I have already mentioned that the only way to divide organisms into sharp groups (other than by using the arbitrary divisions mentioned above which do not yield natural taxonomic groups) is by means of correlated features. It is not so clearly realized that there is no necessary connection between the degree of similarity of organisms and the sharpness with which we can divide them into taxa. The fact that they belong to distinct taxa will not tell us how similar they are, nor will the degree of similarity always tell us if they belong to distinct taxa (since our collection of specimens may be unrepresentative and may omit existing intermediate forms). Nevertheless, it is an observation which seems true for all organisms (even for bacteria and viruses, though some have doubted this), that closely similar organisms commonly belong to one distinct kind, while highly dissimilar organisms usually belong to different distinct kinds. This is fortunate, since it allows us to create hierarchies of taxonomic rank, but it is not logically inevitable.

Adansonian Axioms. These considerations lead to the axioms of Adansonian classification:

1) the ideal taxonomy is that in which the taxa have the greatest content of information, and which is based on as many features as possible.

2) every feature is of equal weight in creating natural taxa.

3) overall similarity is a function of the proportion of common features.

4) distinct taxa are based on correlated features.

One of the most promising new fields is likely to be the application to these concepts of that field of mathematical logic which is called set-theory, since it is sets of organisms and characters that we are concerned with. A start has been made by Gregg (1954), but the details are likely to prove more complex than he thought, owing to the fact that we cannot insist that any particular feature shall by definition be always found in all members of a taxon, a concept discussed by Beckner (1959) and called by him "polytypic." This is a consequence of equal weighting of features, and it is also a major difference between the Adansonian and Aristotelian concepts (see Thompson, 1952; Cain, 1959b). One always finds some aberrant individuals, though luckily it is usually easy to find some features which are constant for most practical purposes. Since natural taxa are established and ranked by the overall similarity of their members, we can only define them as groupings whose members show a certain degree of overall similarity. We can attempt to define them as sets composed of all those elements which share x or more features out of y features, where x and y are large numbers, but in which an ele-

ment may have any combination of features as long as the total number of features shared with every other element of the set is x or more. This definition is not entirely satisfactory; it leads, among other things, to overlapping taxa which cannot always be fitted into the conventional hierarchies. It is slightly different from Beckner's definition of a polytypic class. It is plain that a good deal more study is needed on the logical and mathematical properties of natural taxonomic groups. Some recent work by Maccacaro (1958) on these lines may lead to interesting developments.

It is not yet generally realized that Adansonian methods yield virtually the same classifications which have in the past been achieved by the laborious process of continual taxonomic revisions, sometimes extending over many years, in order to remove their inconsistencies and absurdities. When we do this we are simply removing the added weight which had been misguidedly given to the so-called key features, and are thus approaching equal weighting. The Adansonian method achieves this result at one step. It also allows us to measure objectively the differences in taxonomic rank which we observe. It is true that some conceptual difficulties still remain, notably over the precise definition of taxonomic groups, but most of the other difficulties are concerned with how we may best represent in simple form the intricate and multidimensional relations which are given by Adansonian techniques. Some, such as the models described by Lysenko and Sneath (1959), are fairly simple. Others, such as principal component analysis and factor analysis as applied by Sokal (1958a, b), are mathematically sophisticated. We also need further studies on the subject of hierarchies for it is quite possible that the hierarchical method is not the ideal way of handling taxonomic groups.

Definitions of Taxonomic Categories

There has recently been a preoccupation with the definitions of taxonomic categories. These center about two main topics. The first is what sort of thing a taxonomic group is. The second is the much-vexed question of what a species is.

The Concept of a Taxon. We have seen from the earlier discussion that natural taxa (as opposed to taxa consisting of other units but treated as taxonomic groups) are groups of organisms which share a large number of similar features. But this is only half the truth. A mouse, a rabbit, and a horse share many features, but the group mice plus rabbits plus horses is *not* itself a natural taxon. It is only a part of a taxon—part of the taxon *Mammalia*. Quite clearly a natural taxon embraces *all* of the organisms whose overall similarity comes within certain limits. It is therefore a certain kind of grouping, just as a sidewalk is the whole of a stretch of paving and not just a few scattered paving stones. It is wrong to think of white rats as a natural taxon, *Rattus albus*; they are not a natural taxon since all the rats which are white are included, and this means all white rats of all species of rat. Such a category is a part only of the natural taxon, the genus *Rattus*. We do not in fact make this elementary mistake in ranks above the species level; we recognize that "white carnivores" (white cats plus white dogs plus polar bears, etc) is not a natural taxon. But there seems to be a tendency to forget this in ranks below the species. This is the primary point in the question of whether ecotypes, geographical races, and so on, are to be considered as natural taxa. They may indeed be so, but to be natural taxa their members must exhibit greater overall similarity between themselves than they do with members of nearby groups. Otherwise we may hide natural taxonomic groups (such as valid subspecies, which despite the objections of Wilson and Brown, 1953, are theoretically possible) under false taxonomic divisions. This means in prac-

tice that below that taxonomic level at which we find blending and hybridization between populations (conventionally the specific level and below) we have two different kinds of category,—the first, "natural" or "true" taxa, not sharply defined, but nevertheless of lower rank than "species," and second, "false taxa" which are essentially without rank, since they cannot be arranged in hierarchical order. It should be noted that false taxa can be defined upon correlated characters in the same manner as true taxa. This can happen, for example, where we have an unrecognized mutation showing many different effects. White cats and long-haired cats are examples of two false taxa, since there is no way of deciding if one category is of higher rank than the other. It is impossible to force these rankless categories into a hierarchical system of taxa or into one using hierarchic nomenclature, and we should not try to do so. All the Codes of Nomenclature are ambiguous on this point, and it needs urgent attention; the categories in question are, in the main, these below *subspecies,* which in botany at any rate are very numerous.

What is a species? There has lately been a revolt against restricting the concept of the species to mean a genetic isolate (somewhat variously defined in detail). Nowhere has this been more cogently argued than in the outstanding review of Sonneborn (1957). This has reopened the question "what is a species?" Historically there have been at least four different ideas which have been called "species" (see Andrewes and Sneath, 1958). Linnaeus and others of his time meant a kind of creature which was distinct from all other kinds, without known intermediate forms. In higher organisms this distinctness is generally due to lack of interbreeding between the kinds, so the second definition, the genetic definition, was proposed. Thirdly, the phylogenist thinks of a species as a section of a *gens,* i.e., a distinct kind of creature extended in time (he cannot tell if his fossils interbred or not, so a genetic definition is inapplicable), and although the border between an ancestral and a descendent species is obviously arbitrary, yet at any one time they were distinct from other kinds. Fourthly, some use it frankly as a subdivision of a genus, based on estimates (usually morphological and usually intuitive) of similarity, and this usage is common in the treatment of asexual or clonal organisms. Now you see that the question "what is a species?" has turned into another one. The real question is "what sort of thing shall we call a species?" It is clear that only the first and the fourth usages are applicable in practice to all kinds of creatures, and only these can claim to be general taxonomic terms. To avoid ambiguity they need qualifying with prefixes in the manner of Cain (1954). The only definition of a species which everyone agrees upon is "that level at which I give binomial names," the "binom" of Camp (1951), and few have realized that this is the central point. If we are indeed going to use binomial names for all creatures (and all the Codes of Nomenclature and almost all biologists agree that every creature must have a generic and specific name,—with reluctant exceptions for hybrids and viruses) then "species" must be a term applicable to all kinds of creatures, whether sexual or asexual, and whether fossil or not. The geneticists have made a taxonomic term into a genetic term, thereby not merely narrowing it, but altering its basic concept, which is far more damaging. Quite clearly, *either* we agree that all creatures have a generic and a specific name and employ a species definition which everyone can use, *or else* we admit that the species is useless as a general taxonomic term, invent a new term such as the *series,* and change the rules so that creatures have generic and serial names, or even, as Cain (1959b) has suggested, abandon binomial nomenclature altogether. Unless this reform is made, workers in groups outside the predominantly

sexual organisms will go their own way. Bacteriologists, for instance, ignore the genetic definition of the species and employ the binom instead, and they find no application for the definition of "subspecies" as a geographical race, while virologists are most reluctant to take up binomial nomenclature at all (see Andrewes and Sneath, 1958). But such lack of uniformity cannot be to the advantage of biology as a whole. The most comprehensive reform of species nomenclature is the deme terminology (Gilmour and Gregor, 1939; Gilmour and Heslop-Harrison, 1954), badly misunderstood by many workers, who have used "deme" only for a geographically definable population of sexually reproducing organisms.

There is an advantage in having a name for every "distinct kind" of creature other than the most trivial variants, though, as Simpson (1945) says, they may not all need formal names. If, as in *Taraxacum* and *Rubus*, there are thousands of distinct kinds (in these instances apomictic kinds) we could press into use the trinomial, perhaps under modified rules, for the smallest distinct kind, and cease to use it for indistinct geographic or ecological forms, for which we could use new terms. The terms forma and variety would do for the rankless categories, and it might be best to use only vernacular names for rankless categories, a practice followed by geneticists in naming mutants and now also agreed by horticulturalists for cultivated varieties of plants (see International Code for Cultivated Plants, 1958). It seems to me that with names for genus, subgenus, species, subspecies, varieties and formae, even the most exacting workers would have enough opportunity for their nomenclatural imagination! These suggestions are very similar to those of Edwards (1954).

Phylogeny

Probably no question, after the question of equal weighting of features, gives rise to more argument than the question of whether natural classification should be phylogenetic. There is a real danger that evolution, which attempts to explain the occurrence of diverse organisms without recourse to authoritarian views, may become itself an authoritarian creed for some people, so that anything which they imagine to reflect on their ideas of evolutionary theory is met either with dogma or ridicule.

It is often said or implied that taxonomy should be based on phylogeny. The truth is that to all intents and purposes phylogeny is based upon taxonomy. If we do in fact deduce the phylogeny from the taxonomy, it is clearly ridiculous to maintain that we should deduce taxonomy from phylogeny. The basic assumption involved here is that organisms which are very similar are likely to be closely related as to ancestry, and *vice versa*. For this assumption we have ample evidence in creatures which we can observe to reproduce themselves, and this is the source from which the assumption sprang. It is also the very same assumption that the phylogenist must make whenever he tries to reconstruct a phylogenetic tree. After all, if I wish to know the probable ancestors of living horses, I do not go to the fossil echinoderms and assert that a sea urchin is a fossil horse; I pick a fossil which shows considerable similarity to living horses. In other words, from an intuitive estimate of their similarity—a taxonomic estimate—I deduce a phyletic relationship. If you prevent my taxonomic estimate, by blindfolding me, I would have no idea of the phylogeny of the specimens; obviously, therefore, I could never deduce their taxonomy either.

This crucial point has lately been given some consideration by Cain (1956), Cain and Harrison (1960b), Thompson (1952), Bigelow (1956), Borgmeir (1957), Michener (1957), and Ehrlich (1958), who lucidly demonstrate that overall similarity is independent of phyletic relationship. For a considerable time Simpson has been saying much the same thing (e.g., Sim-

son, 1945). An excellent critique by Sporne (1956) shows, to my mind convincingly, that without a fossil record, our phylogenies are wholly speculative, since we then have no method of knowing (from a study of living forms alone) which of the forms are more primitive—that is more like the ancestor of the group—and which are less so. The point is really very simple; if we estimate the similarity of living forms from their characters we can only assume that their phylogeny is a reflection of their taxonomic similarity, just as we deduce from a cross section of a shrub the probable way in which the branches arose below that section. Similarity is a dimension which has no necessary reference to time. Any attempt to use *some* of the characters to deduce the phylogeny while ignoring others is merely circular reasoning, since our judgment of which of the features are of phylogenetic importance and which are not is guesswork. This may be illustrated by an example: suppose we assert that in humans the vestigial appendix is of no phylogenetic importance. This may sound reasonable, yet the very fact that it *is* vestigial is highly important to survival; if a man had a large appendix like the herbivores he would certainly die of suppurative appendicitis. Similar difficulties apply to most if not all features. Our guesses on phyletic importance are no more convincing than are guesses on the relative importance of features in taxonomy; in both instances the successful guesses are derived from intuitive estimates of overall similarity between the organisms, and we then select the characters which are in best accord with these estimates.

Convergence. One of the arguments against this unorthodox point of view is that it does not take into account the possibility that there may have been, at times, convergence in evolution. This term is only meaningful in our present context if it means overall convergence in most of the characters and not just convergence in one organ (for in the latter event we have the majority of the creature from which to assess its probable phylogeny and its taxonomic position). This convergence may indeed occur, but consider the difficulty of proving that it did. To take a ridiculously extreme example, but one which well illustrates the principles involved, suppose one set out to prove that although the horse was descended from early mammals, the donkey was descended from birds. One would clearly require a sequence of fossils so detailed and closely spaced in successive strata that one could convincingly trace every transition between an undeniable fossil bird and an undeniable fossil donkey, without *any* point at which one could make a mistake in the chain of ancestors. We could not solve the dilemma by looking at donkeys for relics of avian features, for either we would not find them (because, as we would expect from our postulates, convergence had taken place in relic characters as in the other characters), or if we did, we could not prove they were indeed relics of avian ancestry and not the product of independent evolution. Whether convergence in this sense ever occurs is an open question. It seems wholly improbable that it can occur between stocks so widely different as those in this example, but with some closely-related stocks, for example in birds, the question is really acute. We have few adequate fossil records, and none have yet been examined by any acceptable mathematical method for obtaining overall similarity. To use again the analogy of the shrub, how can we prove that two adjacent twigs arose from two widely separated branches if we cannot trace back these twigs in considerable detail down to their parent trunk? We have precisely the same logical problems in cases of parallel evolution, and in determining whether a certain taxon was in fact monophyletic. Michener gives an excellent example of this in his paper of 1957.

We can summarize by saying that

though it would be very interesting to know the true phylogeny of our taxonomic groups, taxonomy cannot be based on phylogeny, and we must just admit that in most instances we have not enough fossil evidence to determine the phylogeny. The implication of this section is quite clear—instead of attempting logical impossibilities, phylogenists would greatly profit by applying quantitative taxonomic techniques to their fossils. The amount of evolution must be measured as the amount of change in the characters of the organisms in question, i.e., in the overall taxonomic similarity between them. They could thus achieve an objective measure of the degree of evolution which has occurred. This would open up a whole new field in measuring evolution rates by answering the call of Simpson (1944) for a way of doing this. The attempts by Kurtén (1958) and Olson and Miller (1958) do not meet the need adequately, either because too few features are employed, or because those chosen are given unjustified *a priori* importance. In the next section a simple example is given, using data on fossil fish taken from the work of Olson and Miller.

Quantitative Methods in Taxonomy

We have already discussed the idea that orthodox taxonomy is based on the concept of similarity between organisms—what is also called affinity, or closeness, or resemblance, or *phenetic* relationship (not phyletic relationship, see Cain and Harrison, 1960b). We also know that in all branches of science there comes a point at which one must attempt to measure the things one deals with. This point has, I believe, now come in taxonomy. I shall not discuss those methods intended to discriminate or identify established taxonomic groups, but only those which estimate overall similarity.

In the last few years five methods have been proposed in some detail, that of Sokal and Michener (Michener and Sokal, 1957; Sokal and Michener, 1958), that of Cain and Harrison (1958), that of Rogers and Tanimoto (1960), that of Sokal (1961), and one which I proposed myself (Sneath, 1957b). These have not been the earliest attempts in this direction. Among earlier methods have been those of Pearson (as early as 1909), modified by Mahalanobis and Rao (see Rao, 1948), Forbes (1933), Anderson and Whitaker (1934), Anderson and Abbe (1934), Sturtevant (1939, 1942), James (1953), and more recently Stallings and Turner (1957). These earlier methods have not, as far as I know, been developed sufficiently to meet the logical and practical needs of such a technique. It seems that the main stumbling-block has been the uncertainty of how to weight the features. This is removed if we agree to count every feature as of equal weight, though curiously enough it turns out that provided we employ a large number of features a statistical consequence is that the effect of weighting some of them becomes in general quite small. The first five methods referred to above do, in practice, give every feature equal weight, and justify this step on several different grounds. They may therefore be said to be Adansonian in their basic philosophy, though several of these authors have certain reservations about equal weighting. These methods have been successfully applied in many groups of organisms, such as insects (Michener and Sokal, 1957), man (Cain and Harrison, 1960a), plants (Rogers and Tanimoto, 1960; Morishima and Oka, 1960), and bacteria (Sneath, 1957b; Sneath and Cowan, 1958; Hill, 1959; Cheeseman and Berridge, 1959; Liston and Colwell, 1960; Talbot and Sneath, 1960; Pohja, 1960; Bojalil and Cerbón, 1961; Colwell and Liston, 1961).

This is not the place to describe in detail the methods, but, briefly, all of them are based on elementary forms of multivariate analysis, a technique which has been principally used in psychology, and in ecology (e.g., Goodall, 1953; Williams and Lambert, 1959) and also, interestingly enough, in linguistics (Ross,

1950). All of the methods compare every organism with every other organism in the study, and then produce a figure which represents an estimate of overall similarity for each of the comparisons between pairs of organisms. Each method employs as many characters as possible, and for practical purposes they all need electronic computing machines to do the extensive but repetitive calculations. These computing machines are now becoming widely available, and there is no reason why taxonomists should not use them. Three of the methods carry the process a step further by forming taxonomic groups which represent higher taxonomic ranks.

Comparison of the Methods. These methods are likely in practice, as far as I can see, to give almost the same taxonomic results. This tentative conclusion is illustrated by Figures 2 and 3, which show good concordance between two methods applied to the same data. Which method should be chosen is therefore probably dependent mainly on the nature of the study. The methods of Sokal and Michener (1958), Cain and Harrison (1958), and Sokal (1961) can employ continuous variables for analysis, while those of Sneath (1957b) and Rogers and Tanimoto (1960) employ systems of counting matches and mismatches between attributes and thus yield coefficients of association. The latter are therefore particularly suitable for data which are mainly in a 'yes-or-no' form. By suitable processing of the raw data any of the methods can be used on any given material. Two points are worth noting. One is concerned with weighting of features, the other with the primary elements which are analysed.

The method of Sokal and Michener (1958) uses as its measure of similarity the familiar statistical correlation coefficient. The length (or other measurement) of an organ is broken into a number of arbitrary ranges, and if there is a great range of length in this organ the overall effect is to give the data obtained from this organ rather more weight than data from organs which do not vary much in their size. The method of Cain and Harrison has the reverse effect: the Mean Character Difference of these authors is based on the percentage difference when the largest example in the sample of specimens is given the value of 100%, and this on the average gives more weight to the less variable organs. This dilemma is to some extent circumvented in the methods which employ coefficients of association. In any event, it seems to be fairly clear from standard statistical theory that the end result is not likely to be very different whichever method we choose, provided, and this is important, that a *large number of features are analysed.*

The other point concerns the units which are to be analysed. If the group to be analysed has not been thoroughly studied, we may have 'poor' or 'bad' morphospecies, and it is then essential to study single specimens in order to create valid morphospecies. After this it is permissible to handle the species as the units for a second analysis. The most illuminating illustration is perhaps again that of arranging books—if we handle them in bundles we can do so if each bundle has been properly arranged before being tied up, but if the bundles were never properly made in the first place, we must cut the string and sort the books individually. My own view is that so much depends on the taxonomic validity of the lower taxa on which the study is based that it is of great importance, even in apparently well-known groups, to check this point first. If possible the type specimens (or in bacteria the type strains) should be used in this checking analysis. One must bear in mind that particularly with microspecies, cryptic, and sibling species the range of variation within each species may, at least in theory, be greater than the variation between the modal forms of the species themselves. This could lead to the unsatisfactory situation in which the species

are "false taxa" in the restricted sense used in an earlier section, with the immediate practical result that the similarity between the species in a quantitative analysis will depend entirely on what individuals are taken to typify these species.

Comparative Serology. Another technique which also gives a quantitative estimate of taxonomic similarity is the technique of comparative serology, developed greatly in recent years by Boyden and his colleagues, and excellently reviewed by him (Boyden, 1942, 1953). The degree of serological resemblance between the serum of one animal and the serum of another animal, measured by means of antisera, is thought to depend upon the degree of similarity of the numerous chemical groupings in the serum proteins of the organisms. It therefore reflects the overall similarity between these proteins, and thus yields an estimate of similarity based on many chemical features. It can be applied to other proteins or to plant material (e.g., Mainardi, 1959; Chester, 1937). We expect, from the quasi-random nature of large samples of features, that such a serological measure of similarity will correspond quite closely with overall similarity as estimated by mathematical analysis of morphological or other features. In practice this seems to be true, for the agreement with traditional systematics based mostly on morphological resemblance is generally very good. There are a number of practical and theoretical difficulties to serology, but undoubtedly serology is of great significance and worthy of wide use. The relation between serology and genetics is also very interesting (e.g., see Irwin, 1959). It has the advantage of giving quick estimates without mathematical complications, and may well prove to be very useful in preliminary as well as advanced taxonomic studies. The gel diffusion precipitin methods may be excellent for much of this work (see Ouchterlony, 1958; Crowle, 1960; Gell, Hawkes, and Wright, 1960). Other new techniques such as paper electrophoresis of proteins (e.g., Sibley, 1960) or of tissue components (reviewed by Wright, 1959) are of great promise in taxonomy, but do not themselves yield estimates of similarity without mathematical analysis.

Rank. One of the important implications of quantitative methods is that it affords an objective measure of taxonomic rank. By drawing lines at a given similarity level, we can pick out the taxa which possess the rank associated with that level. At present we have no standards for ordinal, familial, or generic rank, but there is no reason why workers in certain fields should not agree upon the similarity levels they will use. The exact figures will depend upon the selection of features used in a study. Although a large sample of features cannot be considered a strictly random sample of all the features of the organisms, yet there appears to be a close correspondence in the similarity obtained from one sample and that from another sample, and these samples are therefore quasi-random. This seems true of all kinds of organisms, even bacteria and viruses, and as can be seen from the study of Florkin (1949) we find close correspondence between morphology and biochemistry whenever detailed work has been done. This means that we can compare two different surveys if we have sufficient specimens in both of them, and we can then calibrate the similarity scales against one another. A very simple method, which could undoubtedly be greatly refined, is given by Sneath and Cowan (1958).

Example of Numerical Systematics Applied to Phyletics. An example of how quantitative methods of taxonomy can be applied to fossils is given below. The data are on the Eocene and Paleocene fish *Knightia* given by Olson and Miller (1958, Tables 84–87). Four samples, I to IV, are given, representing four epochs in the evolution of what is probably a single phyletic line, sample IV being the oldest. The characters used were all measurements

of the size of various organs, as shown in Figure 1. In order to keep the analysis small, only the first ten individuals of each of the four samples were employed, and three characters (Sp 13_h, Sp 21_h and C 11_l, which were not recorded for all the fishes) were omitted. The character *length* was omitted and the remainder were converted into the percentage of the length of the individual in question. Thus specimen 1 of sample 1 had a total length of 46 mm, and the mandible length was 6.0 mm. This becomes: mandible length = 13.04% of total length. The data were thus converted from millimeters into proportions, and these proportions were analyzed as described below.

Two statistics were used to obtain estimates of overall similarity. The first was the Mean Character Difference (MCD) of Cain and Harrison (1958). In this the largest value found for each given character among the 40 fishes is taken as 100%, and the other values are expressed as percentages of this. The mean difference, without respect to sign, is then obtained for each comparison of every individual fish with every other. The other statistic used was the correlation coefficient which was employed by Michener and Sokal (1957). The proportions referred to in the last paragraph were first expressed as percentages of the mean of the value of the character in question in the 40 fishes, and the correlation coefficients were computed from these. A part of the two similarity matrices is given in Tables 1 and 2, and shaded diagrams of the full matrices are given in Figures 2 and 3. These matrices express the degree of overall similarity between every individual fish and every other; the dark tones indicate close similarity and the light tones indicate dissimilarity. It can be seen that the two statistics give very similar results in general, with a few exceptions which are discussed below. The means for the four samples are given in Table 3.

From the similarity values the individual fish can be arranged in a pattern

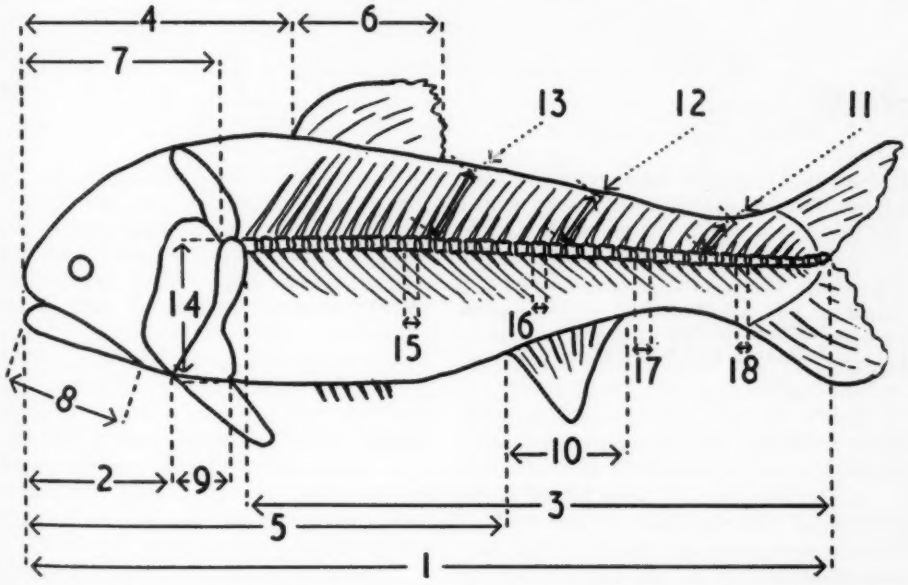

FIG. 1. Characters of the fish *Knightia* employed in the analysis (redrawn after Olson and Miller, 1958).

TABLE 1—COMPARISON OF SPECIMENS OF *Knightia* (SAMPLE 1 ONLY): % MEAN CHARACTER DIFFERENCES.

	SPECIMENS									
SPECIMENS	1	2	3	4	5	6	7	8	9	10
1	0									
2	5.35	0								
3	6.07	6.98	0							
4	5.86	4.80	6.86	0						
5	6.46	4.76	5.79	4.29	0					
6	7.40	6.25	9.11	7.57	5.83	0				
7	7.48	4.23	7.29	4.38	4.10	6.71	0			
8	7.52	6.53	7.71	6.81	4.80	5.89	6.04	0		
9	8.82	5.03	8.82	5.53	5.89	5.05	4.89	7.58	0	
10	9.85	7.64	7.25	6.43	5.20	5.76	6.46	6.93	6.46	0

Mean = 6.37%
Range = 4.10–8.85%

TABLE 2—COMPARISON OF SPECIMENS OF *Knightia* (SAMPLE 1 ONLY): CORRELATION COEFFICIENTS.

	SPECIMENS									
SPECIMENS	1	2	3	4	5	6	7	8	9	10
1	1.0									
2	0.46	1.0								
3	0.43	0.26	1.0							
4	0.49	0.60	0.44	1.0						
5	0.31	0.58	0.29	0.61	1.0					
6	0.14	0.48	—0.29	0.32	0.59	1.0				
7	0.08	0.71	0.23	0.58	0.75	0.59	1.0			
8	0.11	0.34	—0.14	1.15	0.53	0.59	0.26	1.0		
9	0.25	0.77	0.14	0.62	0.55	0.73	0.81	0.40	1.0	
10	0.38	0.32	0.40	0.60	0.69	0.58	0.42	0.41	0.52	1.0

Mean = +0.424
Range = —0.29 to +0.81

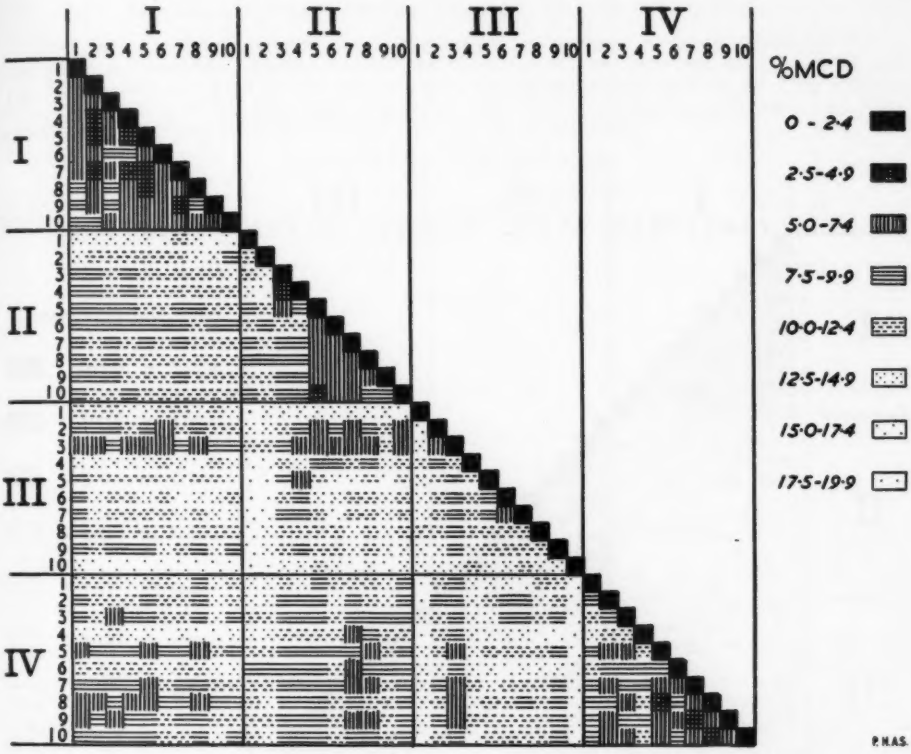

FIG. 2. Diagrammatic representation of the matrix of MCD values, obtained by shading the squares according to the MCD values. I–IV are the samples, each containing 10 fishes.

in two dimensions, and a schematic arrangement (obtained by trial and error, first using the means of the four samples and then fitting the individual fishes), based on the MCD values is shown in Figure 4. This arrangement would best be done by principal component analysis or similar methods, since there is inevitably some distortion in condensing a system of multidimensional relations like this into a few dimensions (Sneath, 1957b). Nevertheless, Figure 4 is probably fairly close to that which such sophisticated methods would give. By expanding Figure 4 vertically in a third dimension, Figure 5 was obtained, which is a schematic and speculative, but not wholly fanciful, representation of the possible evolution of these fishes. Diagrams of this sort and models based on them have an obvious use in teaching and in obtaining a view of the salient relations of the taxa.

This analysis is given only as an example of the methods, for the numbers of features and of specimens is undesirably small, and, as Olson and Miller point out, there may have been distortion during fossilization. In addition there are some drawbacks to the statistics used. Nevertheless, the example is interesting and illustrative.

First, the two statistics give reasonably concordant results: on the whole the fish which are very similar on one technique are also very similar on the other. The biggest differences involve the first fish

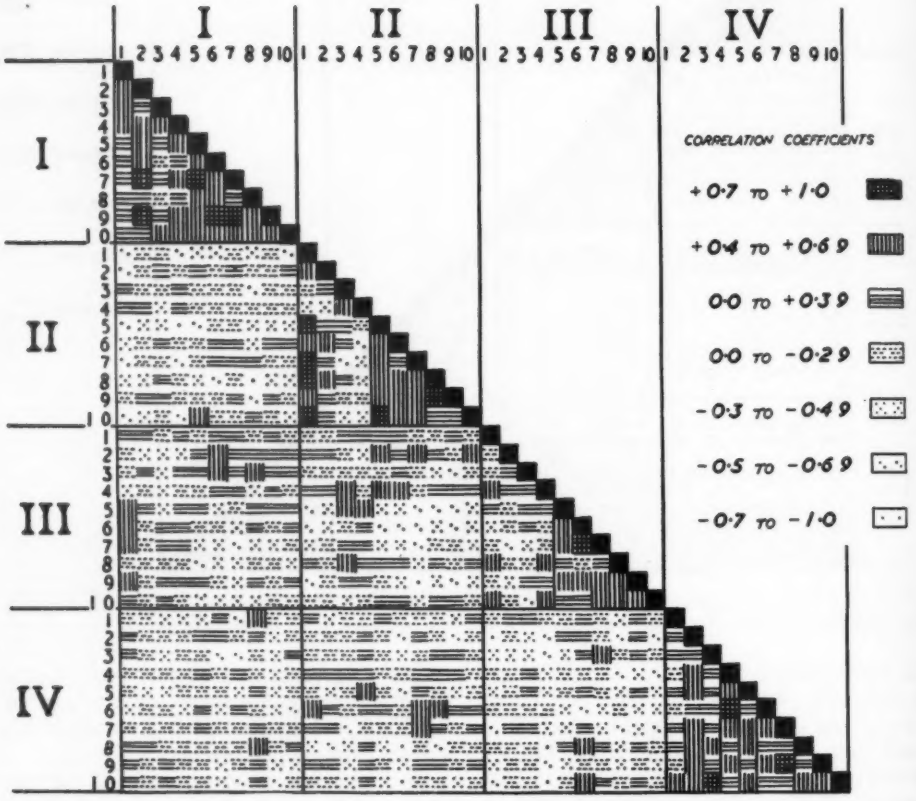

FIG. 3. Diagrammatic representation of the matrix of correlation coefficients obtained by shading the squares as in Fig. 2. I–IV are the samples, each containing 10 fishes.

TABLE 3—COMPARISON BETWEEN THE FOUR SAMPLES OF *Knightia*.

The mean values, and in parentheses the ranges, of the percent Mean Character Differences and the Correlation Coefficients for the comparisons between the four samples are given. The Δ mean values are given for each sample compared with itself (see Sneath, 1957b). The means of the correlation coefficients are the crude means and have not been corrected by Spearman's method (see Sokal and Michener, 1958).

A % MEAN CHARACTER DIFFERENCES.

	SAMPLE			
SAMPLE	I	II	III	IV
I	*6.37* (4.10–9.85)			
II	*10.72* (7.65–15.67)	*8.65* (3.69–15.19)		
III	*11.52* (5.45–17.26)	*12.35* (6.64–19.23)	*11.34* (5.74–15.21)	
IV	*10.26* (5.64–16.25)	*9.92* (5.86–14.76)	*12.40* (5.79–19.96)	*8.00* (4.07–12.90)

B CORRELATION COEFFICIENTS.

	SAMPLE			
SAMPLE	I	II	III	IV
I	*+0.424* (—0.29–+0.81)			
II	*—0.190* (—0.80–+0.35)	*+0.240* (—0.61–+0.78)		
III	*—0.024* (—0.51–+0.62)	*—0.097* (—0.85–+0.62)	*+0.134* (—0.59–+0.75)	
IV	*—0.138* (—0.54–+0.44)	*—0.078* (—0.71–+0.56)	*—0.163* (—0.78–+0.44)	*+0.338* (—0.16–+0.77)

in Sample II and the other fishes in this sample. The correlation coefficient gives higher values for the comparison of fish II.1 with fishes II.5 to II.10 than does the MCD. The statistical explanation is that the covariances for these comparisons are unusually high, owing to the concordance in the algebraic sign of the differences from the mean, while the MCD is calculated without respect to the algebraic sign of the differences. A few other discrepancies are also seen. We do not yet know which of the statistics is a better representation of the taxonomic relations in this instance.

Second, the samples differ greatly in homogeneity. Sample I and Sample IV are both more homogeneous than are Samples II and III. It is not certain what interpretation should be placed on the heterogeneity of the samples, especially since Olson and Miller (1958:274) state that the specimens of each sample evidently all belonged to one species, and that possibly all four samples belonged to a single species. In Figures 4 and 5 the more aberrant individuals have been represented as if they belonged to partly distinct taxa such as subspecies.

Third, it is evident that, despite the heterogeneity of the samples, on the average the members of a sample resemble more closely the other members of the same sample than they resemble fishes of the other samples. This is shown both in Figures 2 and 3 and by the mean values in Table 3: the means for intra-sample comparisons consistently show greater similarity than the inter-sample means. Although none of the characters alone is diagnostic for the groups, this indicates that the four samples represent "natural" taxa; there are a few exceptions to this, but most of these cannot be regarded as statistically significant. However, the fishes III.2 and III.3 show with both the

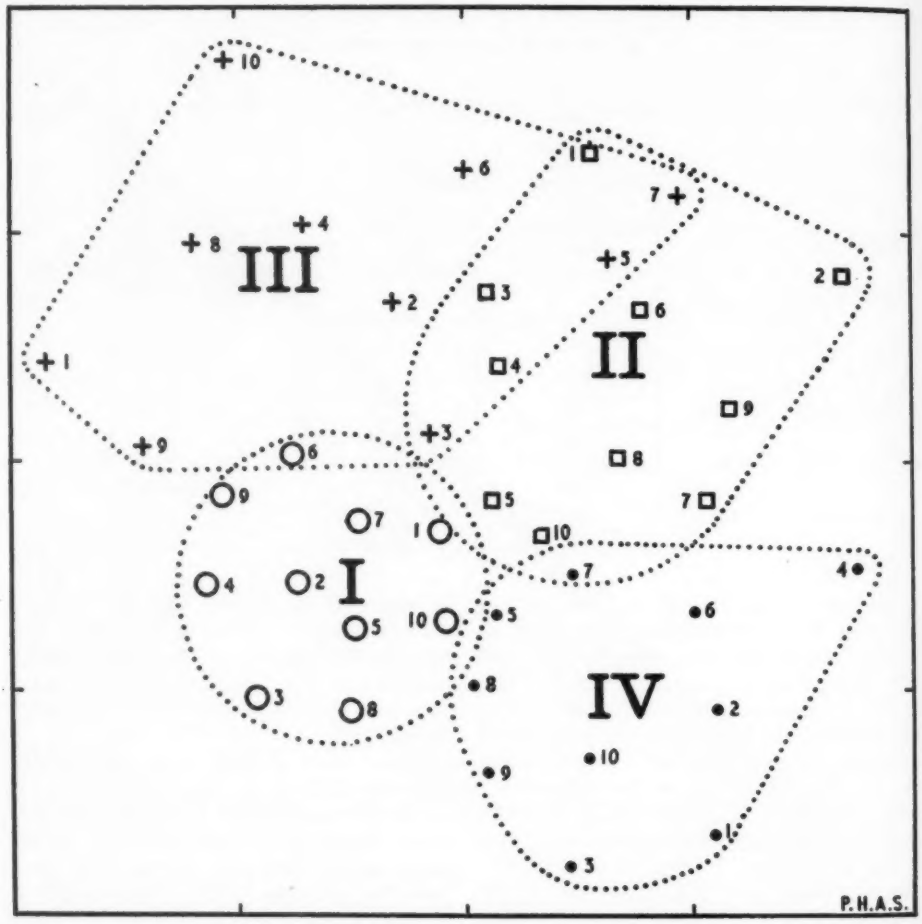

FIG. 4. Arrangement in two dimensions of the individual fish based on Mean Character Differences. The Roman numerals I–IV indicate the samples and the Arabic numerals the number of each fish in the sample.

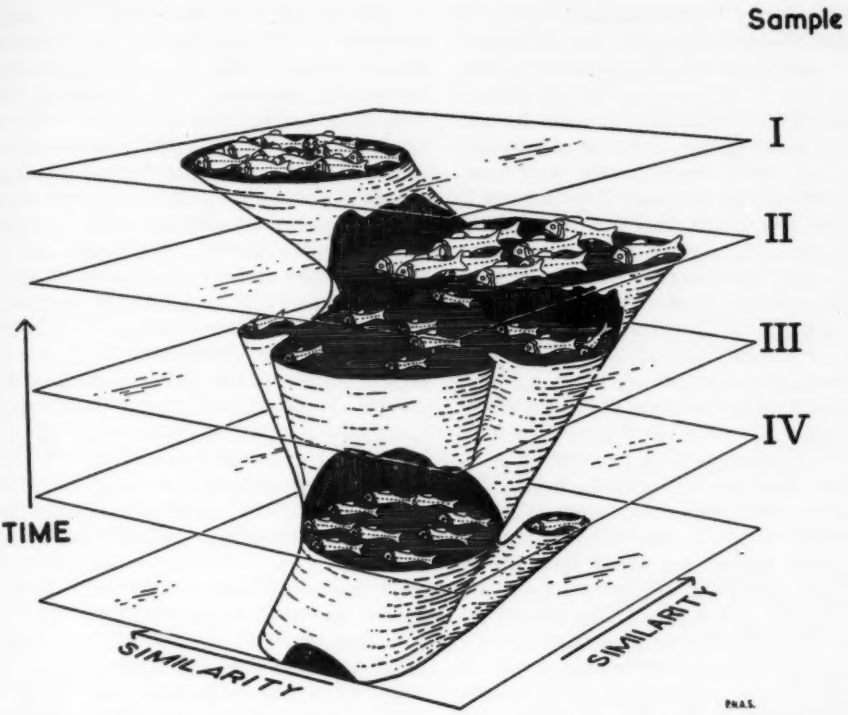

FIG. 5. Schematic and hypothetical phyletic tree of *Knightia*, based on Fig. 4 by extending it in a dimension representing time. The time intervals are shown as equal, though this is not certain.

MCD and correlation coefficients less average resemblance to the other fishes of Sample III than to the fishes in Samples I and IV, and this may be statistically significant. It should be noted that in this material, as with much fossil material, it is uncertain whether the samples represent a wide range of ages. Some fish in a sample may be young and others old, and we would then expect that young fish showed in their bodily proportions a greater similarity to other young fish than they did to adult fish, (and *vice versa*). In this particular example this effect does not appear to be marked since there is no significant correlation between the length of each fish (which was used as the most appropriate index of age) and the similarity indices compared with other fish in the same sample. However, the mean lengths of the four samples do vary considerably, and are as follows: Sample 1, 40.9 mm.; Sample 2, 78.2 mm.; Sample 3, 26.7 mm.; Sample 4, 58.9 mm. With the present data we cannot say how much of the mean similarity between the four samples may be plausibly attributed to a possibility suggested by these figures, that Sample 3 were mostly very young fishes and Sample 2 were mostly very old fishes.

Fourthly, it is also seen from Table 3 that the mean similarities between the four samples are not far removed from equality in each instance, so that the four samples could be roughly represented in space as the points of a tetrahedron, or, in two dimensions, as the corners of a square. There is somewhat less than av-

erage similarity between samples III and IV, and though this may not be statistically significant, this is shown in Figures 4 and 5 by placing III diagonally opposite IV. Should this in fact be significant, it raises the question of whether there had been a small degree of reversal of evolution from Sample III to Sample II (in order to explain why the descendants of sample III became more similar to their remoter ancestors of Sample IV than to their immediate ancestors). Or possibly the ancestors of a population are commonly an unrepresentative and relatively poorly-adapted section of their contemporaries. In this instance the direction of evolution could have been almost undeviating if the gene-pool of succeeding samples had been mostly contributed by individuals very similar to fishes IV, 5, 7 and 8, III, 2 and 3, and II, 5, 7 and 8. This would imply that there may be repeated burgeonings of forms which are well adapted to the prevailing conditions but are doomed to speedy extinction and which consequently contribute little to the ancestry of succeeding parts of the phyletic line.

It may be said that the use of simple ratios in work of this kind is not ideal. It would certainly be preferable to employ the constants of the allometric curves relating each character with the age of the individuals, since the ratios of the characters will vary with age. Before we can do this we must have some assurance that we are dealing with homogeneous samples of single populations. In this case this is uncertain, as mentioned above, and in addition the number of fishes is too small to obtain satisfactory regression lines by the usual methods of allometry. Nevertheless, as a check on the other results, the regressions were calculated for each sample after plotting the logarithm of character size against the logarithm of the length of the fish (employing this latter character as the estimate of the age). The slopes and intercepts of the regression lines were, as expected, mostly of little significance because of the small numbers of fishes and the considerable scatter of the points about the regression lines. For example, with Sample II the constants for no less than 11 of the 14 characters were evidently meaningless. After excluding Sample II and the constants of doubtful significance in the other samples, the data were too few to warrant any firm conclusions. It is worth noting that the uncertainty of results obtained from allometry does not make meaningless the conclusions drawn from the analysis of the characters of the individual fishes. If we wish to measure the overall similarity between individual fishes, considered as geometrical objects, we can do this from the characters without resorting to allometry. If, however, we wish to draw conclusions about the populations to which the fishes belonged then we must have many more data; we must have sufficient individuals to obtain meaningful regression lines and we must ensure that the samples represent single populations; only then can we attempt to answer questions about the relations of the several populations. These limitations of inadequate fossil material should be kept in mind.

It may be said that this analysis of *Knightia* has raised more questions than it has answered, and in a sense this is true, for the data given are inadequate to answer some of the hypotheses which have been raised. Yet this is no bad thing, for it illustrates both the wealth of information which can be obtained from multivariate techniques, and also some of the unspoken assumptions which are commonly made about paleontological material.

Conclusions

In conclusion, we may ask what is the outlook for systematics. I feel sure it will soon become a quantitative science, and that it will be closely linked to logic, information theory, and statistics. The field of systematics will certainly

widen to include entities like genes, enzymes, and even chemical substances, and of course such life as we may one day discover on other planets. Taxonomic techniques based on multivariate analysis will be increasingly used in fields such as medicine, ecology, pedology, and information retrieval, for in all these we have the basic problem of taxonomy—to array complex entities, whether they are diseases, vegetation, soils, or documents, into 'natural' groups. We may soon be able to read the genetic code of organisms and we shall then be able to compare genomes by numerical taxonomic methods. In viruses this may not be so far off, witness the elucidation of the full structure of the protein of tobacco mosaic virus (Tsugita et al., 1960) which may be a direct expression of a large part of the genome of this virus. The concept of equal weighting can liberate taxonomists from a millstone which has hindered them from developing quantitative methods in the past, while acceptance that phylogeny and similarity are independent, though generally correlated, will then permit the exact measurement of evolution rates. A far better understanding of speciation will be possible with independent quantitative assessment of rank and of overall evolutionary change. The better estimation of the higher ranks will also have far-reaching effects on our views of the evolution of the major phyla. What we now need is work on difficult problems which have scarcely been discussed in quantitative terms, such as those peculiar to fossils, to complex life-cycles, and to those elusive entities of modern biology, genes, viruses, and enzymes. We may hope to see the growth of a taxonomy which is applicable to all organisms at all stages of knowledge, with a unified terminology, which can take its rightful place by the side of evolution as one of the central disciplines in biology.

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Zoogeography of the Coleopterous Family Chauliognathidae

GEORGE W. MISKIMEN

ZOOGEOGRAPHIC philosophy to date has been based primarily on the distribution of vertebrate animals though it would seem that a study of invertebrate forms could also make an important contribution. Recognition of zoogeographic principles can be useful to the better understanding of other disciplines such as systematics and phylogeny. It has opened a fresh approach to my general study of Cantharoidea and has contributed to the delineation of a new family, Chauliognathidae (Miskimen, 1961), as well as suggesting other changes in cantharoid classification which will be treated in future papers.

The fundamentals of invertebrate distribution are substantially the same as those affecting vertebrates, especially the poikilotherms (Darlington, 1948). The salient difference is timing. Almost all present-day insect families and many genera were well established at the close of the Cretaceous period while mammals and birds, on the distribution of which many prevailing zoogeographic conclusions are based, were only in very early stages of their evolution. Relatively few major evolutionary changes have occurred among insects since that time; the principal innovations are adaptations, usually at the generic level, correlated with new food sources made available by the Upper Cretaceous angiosperm expansion (Axelrod, 1952; Dorf, 1955).

Geology and climatology of the past are particularly useful in the understanding of contemporary insect zoogeography because of a paucity of fossil evidence. Such indirect evidence, as well as inferences drawn from contemporary observations, assumes great importance when resolving puzzling geographic discontinuities and distributions. The beetle family, Chauliognathidae, is an especially good example.

Chauliognathids are divided into two tribes, Chauliognathini and Ichthyurini, which are found today in rather restricted localities. The group is admirably suited to zoogeographic study because there are comparatively few species; these agree in generally limited spatial ranges, rather restricted habitats, and relative lack of association with man. Careful survey of their distribution adds materially to the appreciation of relationships between the various taxa, including species.

In this paper, geology and climate will be discussed as a unit, followed by correlation with probable origins and dispersions to give a continuous picture of events leading to the contemporary distribution of Chauliognathidae.

Land Bridges, Geology, and Climate

In a discussion of the distributional geography of many species of plants and animals, land bridges are clearly of importance. Nearly every unusual distribution has had a bridge postulated to explain it by someone, but recent information has reduced the number and increased the certainty of those now generally accepted. The distribution of mammals seems to make impossible a proposed connection across the North Atlantic (Matthew, 1915). Land bridges from both Africa and Australia to South America, via the Antarctic continent, have been proposed, but I believe the present distribution of plants and animals can be most satisfactory explained by Bering Strait, Central Ameri-

can, and Indonesian bridges alone. Distribution of both plants and mammals makes continuous land bridges seem unlikely over the wide expanses of water between South America and Africa and the Antarctic continent, and even if temperature conditions were favorable and there were a series of islands connecting these areas, the islands would have to have been spaced with remarkable exactness to allow passage to certain organisms while excluding others. Also, any such movement would presumably first need to have been in the direction of the Antarctic continent and then away from it against a north to south species pressure gradient, which would reduce the likelihood of success still more. Fish, although at first suggesting southern land connections, can be shown to have arrived by other means (Darlington, 1957). Cretaceous reptiles of South America are no more closely related to those of Africa than to those of North America (Mayr, 1952). Insects presently confined to southern continents, rather than dispersing across land bridges in the southern hemisphere, could equally well have been very widespread and then suffered range restriction to their present southern continental habitat. This seems even more probable when Mesozoic insect dispersion and evolution are considered.

The connections included in the continental drift theory (Wegener, 1924, Grabau, 1940, and Dutoit, 1937, 1944) are difficult to reconcile with geological, paleontological, and zoogeographical evidence, and the theory presents more problems than it solves. Wilson's (1949, 1959) continental accretion theory, although not entirely satisfactory, seems to offer a better basis for positioning of the present-day continents. Bridges now generally accepted by geologists and paleontologists fit the accretion theory very well, but not that of continental drift.

An interesting key to actual temperatures from the late Mesozoic to present times is the position of the 18.5°C. or "coral isotherm" during the coldest month. This is one of the principal factors limiting the northward extension of vigorously growing reef corals. Vaughan and Wells (1943) have shown that most hermatypic or reef corals are quickly killed by temperatures lower than 11°C. for any great length of time. After examining fossil corals, Durham (1950) found that from Upper Cretaceous through Eocene this marine isotherm was located approximately 55° north latitude, a position 1800 miles north of its present latitude of 25° north. During the intermediate Miocene period the coral isotherm reached 40° north latitude. The southward extension of warm water in each case was probably similar to that in the north. The distribution of warm water furnishes an excellent indication of the land climate of those times. Emiliani (1958), in his study of deep sea cores, had indicated abyssal temperatures of 10°C. during the middle of the Oligocene. When contrasted with present day levels near freezing, the effects on climate are readily apparent. High mountain barriers and their climate modifying effects were absent, so it seems reasonable to assume that terrestrial climates were also mild. Thermophilic species certainly would have been easily able to traverse a Bering land bridge under Cretaceous and Eocene circumstances.

Added evidence supporting a mild northern climate is the fossil, temperate deciduous plant associations found within the Arctic Circle in the Yukon Valley as late as the Eocene (Chaney, 1947; Seward, 1933). Similar fossil forests have been found in Spitzbergen at 78° north latitude. Coastal area climates were no doubt further moderated by ocean currents which were probably substantially similar to those of today. Dorf (1957) points out that as recently as late Eocene a subtropical flora extended to almost 60° north latitude on the Pacific coast. Even in Lower Pliocene this coastal boundary was considerably north of its present level.

Chemical evidence also indicates a far wider band of warm climate than is now present. Urey's (1948) figures for the latitude of the Cretaceous "coral iso-

therm" based on a study of oxygen isotopes are in agreement with Durham's (1950) paleontological conclusions. Paleotemperature determinations, based on the oxygen isotope deposition ratio in calcium carbonate, conducted by Lowenstam and Epstein (1954), indicate markedly higher temperature levels in the Cretaceous of western Europe than are now found.

Paleozoic Era

The geological and climatological conditions of the late Paleozoic and Mesozoic, the eras during which beetles are believed to have arisen and spread widely, are much less well known than those of the Cenozoic. However, the types and distributions of fossils, especially marine forms and plants, do shed considerable light. A long period of mild climate extending from late in the Cambrian almost uninterruptedly through to the end of the Carboniferous was brought to a close in the Permian after mountain uplifts and general continental emergence. The ensuing cold, arid conditions severely affected the Carboniferous fauna and flora at all taxonomic levels. The extensive coal-producing Pteridophyte and Pteridosperm vegetation of the Carboniferous including Calamitales, Lepidodendrales, Cordaitales, Sphenophyllales, and Coenopteridales gave way to the more cold and drought-resistant cycadophytes and higher conifers (Arnold, 1947). Durham (1958) found that Permian marine faunal distribution patterns approximate those of Recent times, suggesting that continental temperature patterns also were similar. He considers such relatively cool periods to be abnormal compared to the much longer periods of mild climate during geological history. Brooks (1951) also holds this view and concludes from geological evidence, that average temperate region temperatures fell during the Permian by as much as 20°F.

The cosmopolitan distribution of many animals and coal-forming plants indicates that land bridges were present at least during the Carboniferous. The cold Permian climate persisted into the early Mesozoic but, commencing with Upper Triassic, mountain-leveling occurred. The consequent low topography and shallow seas resulted in mild temperatures throughout the earth. Smith (1927) states that certain reef-building Astraeidae were found in the Upper Triassic of Alaska. Polar ice was sufficiently reduced by the onset of the Cretaceous to cause the most extensive land inundation since Ordovician times. Vast inland seas covered many former continental areas of the world. Such favorable conditions encouraged a great expansion of flora and fauna during the Jurassic and Cretaceous. Empty ecological niches were filled by adaptable organisms which often underwent adaptive radiation to give rise to new lines.

Mesozoic Era

It seems probable that Asia and North America were connected at the Bering Straits for much of the Mesozoic. The Bering bridge and a coincident mild world-wide climate presumably allowed free interchange of species between the eastern and western hemispheres. The essentially cosmopolitan distribution of the ruling reptiles (Darlington, 1957) and of many dominant plants (Arnold, 1947) of the era bears out this conclusion.

Relatively constant Mesozoic land connections between North and South America, followed by long periods of isolation during the Tertiary, are clearly indicated. As a consequence of such isolation, South America is notable as the home of many endemics, as well as an unusual number of primitive relict plant and animal species. Sporadic Cenozoic connections, particularly the present connection dating from Upper Pliocene, have diluted the effect, but the results of long isolation may be plainly seen.

Australia had fairly continuous connections with the Asiatic mainland throughout the Mesozoic as shown by both fossil and modern native forms. During Upper

Cretaceous, the Australian Zoogeographic Region became permanently separated from the Asiatic continent. Further evolution was therefore restricted to lines already present in that region. The present day native flora and fauna are a classic example of evolution under isolation. New Zealand probably never was connected to Australia, as may be seen in its high degree of endemism and apparent lack of dinosaur fossils, otherwise almost cosmopolitan. Terrestrial animals in New Zealand probably have arrived by sea or by air over a long period of time. New Guinea, on the other hand, is a continental island associated with Australia. A warmer climate alters an otherwise fundamentally similar fauna. Great floristic and faunistic diversity is present along mainly altitudinal lines. Extensive Cenozoic mountain building makes an appraisal of past history difficult, but fish distribution in the rivers of southern New Guinea and northern Australia indicate a common watershed (Whitley, 1943), at least during the Pleistocene.

During most of the Mesozoic and early Tertiary, Europe and northwestern Asia were separated from Africa and southwestern Asia by the Tethys Sea; the northern and southern halves of the eastern hemisphere were connected only in extreme east Asia. During this period, fossil evidence indicates that the exchange of species between African, southern Asian, and Australian land elements south of the Tethys Sea was essentially unrestricted. Mesozoic faunistic and floristic relationships were closer throughout this entire area than those between it and the Palearctic or the New World. An exception is the island of Madagascar with its long isolation, apparently beginning in the Oligocene and possibly as far back as the Mesozoic. Existing and fossil faunas do not seem to require a land bridge (Darlington, 1948, 1957). The only known dinosaur fossils found on Madagascar are sauropods which were semi-aquatic and presumably could have easily traversed the Mozambique Channel. The only recent Malagasy representatives of the Ostariophysi which arose during the Cretaceous are peripheral marine catfishes of the family Plostidae. The only other fish are secondarily fresh-water Cichlidae and Cyprinodontidae (Pellegrin, 1933).

Cenozoic Era

The geological record becomes much clearer in the Cenozoic. Many of our principal modern mountain ranges were erected during this period, with subsequent climatic alterations. Geosynclines that gave rise to the Rockies, Andes, Himalayas, Alps, Apennines, and other important mountain ranges are believed by most geologists to have been formed in the late Paleozoic, with an orogenic phase continuing from the Jurassic or Cretaceous through to the massive Miocene faulting. Weathering nearly kept pace with elevation until the Oligocene so there was no appreciable climate change, permitting almost unimpeded species exchange between continents during periods when land connections were present. Hopkins (1959) points out that a Bering land bridge probably existed during much of the Tertiary, the most notable seaways being formed during Middle Eocene, Upper Pliocene, the Pleistocene interglacial intervals, and at present.

During the Upper Oligocene, Miocene, and Pliocene, temperatures fell rapidly (Brooks, 1951), reaching rather cool levels with subsequent wide-spread range restriction and extinctions. Extensive volcanism that occurred throughout much of the Miocene no doubt reduced insolation, perhaps sufficiently to affect temperatures. However, interference of air circulation by newly created mountain ranges no doubt played a major role (Flint, 1947). During the Pliocene the Sierra Mountains were raised from a former plateau, further obstructing air circulation. The effects of cold were accentuated as increasing amounts of ocean water were bound in the form of ice. Chaney (1940) and Axelrod (1956, 1957) considered the geographical

location of Pliocene floras indicative of an environment quite similar to that of the present. Pliocene summers were cooler than those of today, but winters had not reached the low temperatures of Pleistocene and Recent times (Flint, 1947). Pliocene cold set the stage for both Pleistocene glaciation and our present day climate. It seems entirely possible that at least during Upper Pliocene there may have been ice advances so that no sharp climatic transition existed between that period and the Pleistocene.

Cool weather commencing with the Oligocene presumably served to restrict the range of many thermophilic species. Plant and animal associations indicate that the cooling effect was slow enough until the Pleistocene to permit movement of whole associations to more suitable areas (Dorf, 1955). Major extinctions appear not to have occurred until the Pleistocene glaciation which resulted in the extermination of many species, especially those located in such areas as Europe, western Asia, and eastern North America. In these and several other instances many animals and plants were literally driven into the sea or were trapped between the oncoming northern glaciers and those formed in mountain ranges to the south. This may be seen in a comparison of the flora and fauna of east Asia with that of Europe and western Asia. Many groups still surviving in east Asia, which suffered no such entrapment, have been eliminated from the other areas. Plants and cold-blooded animals were particularly affected. Glaciation is customarily blamed for the extinction of many large mammals but it would seem that early man, even with the puny weapons then available, could also have been a considerable factor.

There is some evidence for the submergence of eastern Africa during part of the Eocene, leaving a number of relict species with closer affinities to the Oriental Region than to the contemporary fauna of eastern Africa. The Tethys Sea continued to isolate all but the extreme eastern Palearctic from the Ethiopian and Oriental Regions until the Miocene uplift of the Alps and Himalayas. Invasion from the south after elimination of the Tethys barrier was probably restricted mainly to those forms able to survive an increasingly cooler climate. The Mediterranean Sea, which is but a remnant of the western Tethys Sea, remained as a moderate distributional barrier between Europe and the Ethiopian Region. The Sahara desert also helped block species exchange here.

South America was essentially isolated during the Tertiary although Central American bridges seem to have been formed for short periods during the Eocene, Oligocene, and Pliocene.

Australia and Asia certainly never had a Tertiary connection. During the Pleistocene, New Guinea, Australia, and Tasmania were connected with some species exchange.

Origins, Dispersions, and Zoogeography

Insects have a long history of success dating back to the Devonian in a wide variety of predominantly terrestrial habitats. The oldest beetle known with certainty was recorded from Upper Permian deposits of Russia (Martynov, 1933). The Lower Permian fossil *Tschekadocoleus* appears to represent a link between neuropteran and true coleopteran lines (Jeannel, 1949).

Chauliognathids belong to the superfamily Cantharoidea, found in the relatively primitive polyphagan series Elateriformia. Crowson (1955, 1960) believes that the Elateriformia were derived during the Lower Jurassic polyphagan expansion from Eucinetoid stock, one of three initial off-shoots of primitive Polyphaga. If larvae are an accurate indicator of affinities, the superfamilies Elateroidea and Cantharoidea may also be close to the adephagan superfamily Caraboidea, since the larvae of each group have in common a toothed nasale rather than a labrum. The presence of carnivore-type viscera in many largely phytophagous adults also supports possible derivation from anteced-

ents related to ancestral adephagans. If the Elateriformia are actually closely related to the ancestral beetle stock, they may have originated in the Upper Permian and then greatly expanded their range as new niches opened with the rise of angiosperms during the more favorable warm Jurassic and Cretaceous periods. This is especially likely for thermophilic segments of the Elateriformia, such as chauliognathids. At the moment it appears quite likely that ancestral chauliognathids followed the same initial course of origin and dispersion as their elateriform relatives. Also, the complete isolation of the Australian Region and relative isolation of South America at the end of the Cretaceous, combined with the great species strength in these areas, makes their origin after this period seem quite improbable.

Although certain features such as wing venation, exoskeleton, and genitalic armature are rather advanced, chauliognathids are generally unspecialized. Abdominal segments are more numerous (eight) than those of almost any other beetle group, tarsal number is equal and pentamerous, antennae are eleven-segmented, and internal organs are relatively primitive. Known larvae are exclusively carnivorous as are the adults of many species. The mixture of unspecialized and specialized characteristics found in the family is in accord with the often expressed thought that an entire organism seldom, if ever, evolves as a unit; some parts always remain relatively primitive.

The morphology of the ancestral chauliognathid is conjectural but it seems logical that three characteristics were probably found: (1) symmetrical genitalia, (2) elytra which completely covered the hindwings, and (3) jaws adapted to carnivorous food habits. In short, its appearance would be similar to a modern Australian *Chauliognathus* but with symmetrical genitalia, or like modern members of *Ichthyurus* but with full-length elytra.

Many, but not all, present day chauliognathids have markedly asymmetrical genitalia from which derivation of a simple symmetrical type would be difficult to explain. Asymmetric genitalia, generally uncommon among beetles, are so often found in the Chauliognathidae that they would

TABLE 1—CONTEMPORARY DISTRIBUTION OF CHAULIOGNATHINI

NEOTROPICAL REGION

Area	*Chauliognathus*	*Daiphron*	*Psilorhynchus*	*Molychnus*	*Totals*
Central America	32	7	—	—	39
Patagonia	62	10	—	1	73
Selvas	12	4	2	—	18
Compos	126	11	—	—	137
Pampas	27	—	1	—	27
					294

NEARCTIC REGION

Area	*Chauliognathus*	*Totals*
Southwestern	26	26
Eastern	2	2
		28

AUSTRALIAN REGION

Area	*Chauliognathus*	*Totals*
New Guinea	24	24
Australia	1	1
		25

TABLE 2—CONTEMPORARY DISTRIBUTION OF ICHTHYURINI

NEOTROPICAL REGION

Area	*Maronius*	*Trypherus*	*Belotus*	*Lobetus*	*Pseudo-lobetus*	*Totals*
Central America	2	2	8	1	2	15
Antillian	—	—	—	—	6	6
Patagonia	6	4	3	7	—	20
Selvas	4	—	—	1	—	5
Compos	14	2	1	—	—	17
Pampas	3	1	2	—	—	6
						—
						69

NEARCTIC REGION

Area	*Ichthyurus*	*Trypherus*	*Belotus*	*Totals*
Southwestern	6	—	2	8
Eastern	—	1	—	1
				—
				9

PALEARCTIC REGION

Area	*Ichthyurus*	*Totals*
Japan	5	5
		—
		5

ORIENTAL REGION

Area	*Ichthyurus*	*Totals*
India	43	43
Indo-China	63	63
Indonesia	44	44
		——
		150

AUSTRALIAN REGION

Area	*Selenurus*	*Totals*
Australia	12	12
Tasmania	2	2
		—
		14

ETHIOPIAN REGION

Area	*Ichthyurus*	*Totals*
West Africa	24	24
Ethiopian Plateau	7	7
		—
		31

seem to have been derived early in the family's history. The elytra of modern chauliognathids range from types that expose only the terminal two or three addominal segments to very much abbreviated elytra exposing most of the abdomen as well as the membranous wings. The Ichthyurini and Australian Chauliognathini retain carnivorous mouth parts. Contemporary New World *Chauliognathus* have a remarkable modification of mouth parts which permits their feeding on nectar and pollen. Not only are the mouth parts greatly elongated but an apparently unique, protrusible, tongue-like appendage emanating from the labial palps, utilized in "lapping up" nectar, is present. These changes may be a response to the vast food supply made available by the angiosperms which arose during the Cretaceous. Gressitt (1952) indicates that there may be a relationship between the evolution and dispersal of insects and their host plants. The herbivorous modification apparently occurred at least after the Upper Cretaceous, when the Australian Zoogeographic Region was last linked directly with Asia. Herbivorous habits seem to be derived from an original carnivorous habit since: (1) larvae of all chauliognathids are apparently exclusively carnivorous; (2) Australian Region Chauliognathini, semingly separable from New World forms only because of mouth part differences, have retained carnivorous adult habits during their isolation beginning in the Cretaceous; and (3) the widespread, closely related Ichthyurini are apparently entirely carnivorous as adults and as larvae.

Chauliognathid distribution generally seems to reflect Sclater's (1858) zoogeographic regions. Wallace's (1876) subregional designations, based on broad environmental and topographical differences within regions, do not seem especially useful to an evaluation of the pan-tropical Chauliognathidae. Terms which seem to be more meaningful are used on the map in Figure 1.

Present day distribution suggests that the group is basically thermophilic and hygrophilic although there is evidence for a certain amount of pre-adaptation to rather dry environments (see Tables 1 and 2). Minimum temperatures appear to be of greater importance to distribution than maximum temperatures. Moisture does not seem to be as great a limiting factor as temperature, although moist habitats are clearly more favorable. Eighty-three percent of the known species inhabit areas having an average temperature of at least 15°C. during the coldest months. Ninety-five percent live in areas with an average cold month temperature of at least 10°C. In addition, the habitats very often have relatively high rainfall and humidity. The true percentages are probably higher, since many undescribed species undoubtedly remain in the poorly collected tropical strongholds of the family. Even in New Guinea, where some radiation of tropical forms from warm lowland regions to cooler mountain areas has taken place, known species are found in localities with temperatures and humidity comparable to chauliognathid distribution elsewhere. Unlike many other poikilotherms, the Chauliognathidae have no definitive northern cold tolerant fauna. Only a few scattered species have had the adaptability to meet more severe climates. Because the family is mainly cold intolerant, Pleistocene "glacial refuges" as multiplication centers described by Hennig (1950) and many others, must be viewed with caution. Although many other modern, temperate area forms probably radiated from refuge centers, these would semingly have been intolerable to such generally thermophilic species as the Chauliognathidae. Their post-Pleistocene dispersal presumably occurred largely from regions that remained not only unglaciated, but warm throughout the glacial periods. A very few species have apparently been able to adapt to colder climates such as Japan, northern United States, southern South America, Tasmania, and south Australia. However, there appears to be no extensive pre-adaptation

FIG. 1. Hypothetical distribution routes of the family Chauliognathidae.

to cold climates as is found among so many other invertebrates.

The only chauliognathid known as a fossil is *Chauliognathus pristinus* (Wickham, 1909, 1914). This species was found in the rich insect deposits of Colorado's Florissant shales along with many other present day genera and families, including several closely related groups within the same superfamily. MacGinitie (1953) discussed the Florissant flora and climate, which during the Oligocene was subhumid warm temperate. Lakeside and fluvial habitats had rich vegetation while high ground was occupied by savannah grading into scrub-forest or short-grass prairie in drier areas. It is especially interesting to note that fossil insect associations of the Florissant are very much like these of similar modern habitats, a demonstration that the climatic tolerances of many insects have not changed appreciably.

Even without additional fossil evidence chauliognathid zoogeography can be pretty clearly understood from the present discontinuous distribution, the climatic limitations of the family, and the geological and paleobotanical evidence already at hand. For example, the discontinuities give absolute time limits for dispersion in many instances.

It appears likely that the family arose during the early Mesozoic in the area now occupied by Indo-China and India, south of the then existing Tethys Sea. Members of the newly arisen taxon no doubt spread rapidly throughout most of the world because of the great extent of the Mesozoic tropical areas, and the many unoccupied ecological niches. Land bridges at various times during the Mesozoic allowed entry by various elements into both North and South America as well as into Africa and Australia. Lack of substantial barriers probably permitted wide distribution of species. Until the mid-Cretaceous, the only notable Mesozoic distribution barrier was the Tethys Sea, which separated what is now the Palearctic from the Ethiopian and Oriental Regions except for a broad connection in eastern Asia, over which travel by insects may have been quite easy.

It would appear that the ancestral stock of the Chauliognathidae, probably characterized by symmetric genitalia, long elytra, and carnivorous food habits, quickly gave rise to two basic types. The first, Chauliognathini, soon developed asymmetrical genitalia and, originally, probably was the dominant group, spreading widely before mid-Cretaceous throughout the world. The second stock, Ichthyurini, retained most of the ancestral features but today have foreshortened elytra. The range extension of the Ichthyurini was slower; they reached Africa before the Eocene and North America after its Cretaceous separation from South America. Evidence supporting this hypothesis includes the marked species strength of the Chauliognathini and relative weakness of the Ichthyurini in the Australian and Neotropic Regions. Since the only members of the tribe Chauliognathini now found in the eastern hemisphere inhabit the Australian region, especially tropical New Guinea, one can assume that their arrival occurred prior to mid-Cretaceous, since after that time that area was entirely cut off from Asia and Indonesia. This complete isolation seems to have been an important factor in the survival of Australian Chauliognathini. In the western hemisphere, the Neotropical Region remained cut off during most of the Tertiary. Relative isolation until late Pliocene and a change in food habits enabled a strong fauna to develop, again in the tribe Chauliognathini. In this case also, the time of arrival seems necessarily prior to mid-Cretaceous. The Ichthyurini, on the other hand, have relatively few representatives in these two areas but are especially strong in the Old World Tropics. Their Australian representatives consist of a peripheral endemic genus of which 14 species have been described. In the Neotropics there are five genera, three of which are endemic and the others nearly so, with only 69 known species. The dominant genus of the subfamily, *Ich-*

thyurus, is totally absent from both the Australian and the Neotropical Regions.

Many modern insect families and genera were in existence during the early Tertiary (Wickham, 1909, 1914). A number of these, however, have been subjected to considerable range restriction. Population pressures, topographical and marine barriers, and especially climate severely curtail range expansion of animals and plants. Only when one or more of these factors are reduced or eliminated can ranges be increased. If they are magnified, ranges contract.

Groups with innately low vagility have an especially great disadvantage during periods of climatic range restriction. They are often exterminated, or, at best, are eliminated from former ranges by more successful competitors which reinvade with greater rapidity after easing of climate conditions. Chauliognathids are very poor fliers, seldom rising far enough above the earth's surface to be caught up and carried by wind currents, which may partially explain their inability to expand their present ranges and their absence from otherwise suitable isolated habitats such as Madagascar, New Zealand, and the strictly oceanic Pacific islands.

Apart from the obvious limitation imposed by water barriers originating in mid-Cretaceous, the climate of the early portion of the Tertiary, probably had relatively little effect upon chauliognathids. The early Cenozoic may have been the scene of extensive species radiation in response to increasingly diverse available foods in the form of angiosperms, which were attaining their present-day supremacy at that time (Li, 1952). The first Tertiary happening of consequence to chauliognathid distribution was an Eocene submergence of east Africa. Later, after the Ethiopian plateau was raised, the environment of that area was unfavorable to a general chauliognathid reinvasion because of coolnes and dryness. The few species able to enter the plateau evolved along lines unlike those of the more typical rain-forest species of west Africa and those of the Oriental region.

The Tethys Sea barrier persisted until the Miocene uplift. As a result the fauna and flora of the Oriental and Ethiopian Regions, which before that time had no intervening barriers, still have closer affinities with one another than with the Palearctic. After Miocene mountain building and the restriction of the Tethys Sea, some species exchange with the Palearctic took place although it was limited by what is now called the Mediterranean Sea and by the newly formed Himalaya Mountains.

Miocene mountains and volcanism accelerated climate changes originating in the Upper Oligocene. Many plant and animal groups were affected, and chauliognathids were no exception. It would seem likely that, although the Bering Strait was probably bridged by land during part of the Upper Miocene and Middle to Upper Pliocene and at least by ice during much of the Pleistocene, the Chauliognathidae did not have free species exchange between the Old and New World after Middle Oligocene (Simpson, 1940, 1947a, b). Hopkins (1959) believes the Bering bridge to have existed almost continuously during the Cenozoic before this time, except for a probable seaway during Middle Eocene. Temperatures no doubt began to constrict ranges beginning with Middle Oligocene. Nevertheless, the most marked range restriction by cold of the intolerant Chauliognathidae probably occurred during the Pliocene and Pleistocene. The relatively rapid climate changes associated with Pleistocene glacial advances and recessions undoubtedly had an important effect upon the distribution of the Chauliognathidae. Franz (1952) notes that the more frequently environment changes, the poorer the fauna. Chauliognathids, as well as many other animals, were completely eliminated from the western Palearctic, which was almost completely covered by ice during the Pleistocene. In the eastern Palearctic and in the Nearctic, chauliognathids were

simply driven southward where no east-west mountain ranges blocked their paths. Evidence supporting this view may be found in five representatives of the widespread, dominant genus *Ichthyurus* that are now found in Japan, many miles north of their nearest relatives. These are undoubtedly remnants of an originally larger fauna that was isolated on the Japanese archipelago. Pre-adaptation and the milder maritime climate probably contributed to their survival. The area north of the Ethiopian Region became temporarily habitable, but if there was an invasion northward into the Palearctic Region, it must have been short-lived because of increasing dryness in the Saharan and Arabian areas. Reinvasion of the Palearctic via the Eurasian steppes of Russia, was prevented by the same conditions (Uvarov, 1938). The total lack of Ichthyurini in the Mediterranean border area or in the Palearctic is strong evidence for these conclusions.

After the last Pleistocene glacial recession range expansions occurred to produce the present day distribution. Oriental Region Ichthyurini have been limited in expansion northward by the Himalaya Mountains although some species have entered the coastal regions of southern China. However, climate restricts northward extension into the Palearctic.

I believe that at some time after the isolation of the Australian and Neotropical Regions in mid-Cretaceous, the ancestral type of the Chauliognathini was eliminated elsewhere by more competitive species. The identity of the competitors is conjectural; many species could fill the bill. The timing also is unknown. It could have been early in the Tertiary or after the Miocene. The complete absence today of Chauliognathini in the eastern hemisphere except for isolated Australia is strong evidence supporting that view. It also seems probable that they were displaced from the Nearctic at least prior to the Pliocene connection with the Neotropics. It would seem highly probable, if Chauliognathini were not eliminated outside of Australia and the Neotropics, that at least some of the carnivorous Australian-type forms would have survived elsewhere. Central America would seem to be an especially likely place to find this type, but there are only typical South American forms present there today.

While they were isolated, South American forms apparently developed their distinctive herbivorous-adapted mouth parts and new food habits. This change seems to be a major reason for their survival and competitive ability. It is notable that, in many cases, Nearctic invaders displaced Neotropical animal and plant life. Counter-invasion northward is much less common. Apparently the herbivorous habit of Neotropical chauliognathids enabled them not only to attain great strength in the Neotropics but also allowed a substantial invasion of the Nearctic, which was presumably halted only by environmental factors, although this relatively recent invasion may not yet have been completed. Although the Australian forms retain the ancestral carnivorous-adapted mouth parts, they and the Neotropical species are unmistakably of common origin. In this case, isolation actually may have permitted their survival.

The exact relationships of North and South American Chauliognathidae are difficult to determine. Three possibilities exist: (1) North America may have had a considerable fauna throughout the Tertiary, which was restricted to the southwest during the Pleistocene, (2) the present fauna may have been entirely derived from South American forms, or (3) there may be some combination of the first two. The strongest support for the first possibility is the fossil *Chauliognathus pristinus*, though its presence would not necessarily mean that chauliognathids were in the area during the entire Tertiary, since there were links to South America in both Eocene and Oligocene. It is perhaps surprising that only one species was found amidst rather substantial numbers of other, associated insect groups. The paucity of Nearctic species compared to the

very large Neotropical fauna militates against a large North American fauna prior to the Pliocene connection. If there had been such a fauna it should seemingly have been driven southward during the Pleistocene, then expanded its range again under more favorable conditions. Moreover, the chauliognathids have no cold tolerant fauna in the Nearctic as do certain other beetle families (Linsley, 1939), which may be evidence for their fairly recent arrival. Present day distribution of *Chauliognathus* in the Nearctic suggests a Pliocene invasion from South America which was quickly halted by colder climate and glaciation. As the Sonoran area of the southwestern United States became drier, some species were able to adapt to local conditions and are competitive today. These forms are characterized by an average larger size than most Chauliognathini, a quality useful for water conservation. The bound water capacity of such species may be an important factor in their ability to tolerate colder or drier environments. Only two species, *Chauliognathus pennsylvanicus* and *C. marginatus*, having close affinities with Mexican forms, were able to spread east of the Mississippi River. That these have a high degree of adaptability is attested by their range from Florida to Canada. The southwestern fauna could be regarded as "relict" as are a number of other animals in that area. Actually, the true relicts seem to be members of Ichthyurini, especially *Ichthyurus*. It would seem that small numbers of species entered the Nearctic before the Oligocene-Miocene climate changes, established themselves, and then were restricted during increasingly severe weather conditions. Then, after the Pliocene union with South America, representatives in small numbers invaded South America and underwent considerable adaptive radiation, as evidenced by five rather small genera with widely scattered species. Three species from two of these genera then reentered the Nearctic and were sufficiently competitive to spread rather widely, especially *Trypherus latipennis*.

The relatively little research done thus far in the field of insect zoogeography has already resulted in new insight out of proportion to the time involved. Future studies should add much to our understanding of both insect distribution and basic entomology itself.

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Utilitarian Aspects of Supergeneric Names

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MUCH HAS BEEN said and written about the usefulness of scientific names of animals and plants. My views on the subject are by no means original. In fact, they have been expressed repeatedly by many authorities. If this report carries a note of futility it is because my observations over the years lead me to conclude that many taxonomists regard utility with suspicion if not outright hostility.

This conclusion should occasion no surprise, for the taxonomist wants freedom to add to and change his classification according to the results of his investigations and the dictates of nomenclature. The economic entomologist and other biologists who wish to use taxonomic names to communicate knowledge tend to equate utility with stability. This attitude is not unreasonable, because these scientists need a simple, stable system for finding and conveying information. However, no thinking biologist will fail to appreciate the need to change names when species are found to be composite. They will even tolerate the often disruptive changes that result from strict application of the rules of nomenclature. Their patience is worn thin by the taxonomists' uncertainty about the rank to be accorded supergeneric categories. They see subfamilies promoted to families and suborders elevated to orders only to have other authorities either refuse to accept the changes or proceed to institute additional changes of a chain-reaction type. They find that they must use an *oidea* instead of an *idae* ending for familiar family groups and then wonder what was gained by the change. They are puzzled when they discover that one authority includes both bugs and leafhoppers in the order Hemiptera, whereas another restricts Hemiptera to the bugs and places the leafhoppers in Homoptera. They will also find that the Orthoptera and the Neuroptera are similarly divided into suborders which many authorities treat as distinct orders, and will wonder why taxonomists have not reached agreement on the number and names of the orders of insects after 200 years.

However, the category for families presents a far more serious problem when compared with that for orders. With families confusion reigns. One authority will divide Hemiptera (strict sense) into 45 families, another into 52, and still another will concentrate his efforts on one segment of the order and stoutly defend the status of 16 families, whereas presumably less well-informed authorities will recognize only one. In the order Hemiptera, at the present time, one group of taxonomists is consolidating families in the reduvioid complex; another group is busily fragmenting the pentatomoid complex. This situation is not isolated but prevails more or less throughout the class Insecta.

Now why should the lack of general agreement on the rank accorded a category be cause for concern? After all, more is seldom involved than a simple elevation or demotion. Basic relationships do not change. My principal concern is the effect that this lack of stability has on communication of information.

Biologists are using hopelessly antiquated methods to maintain inventories of the earth's biota. Few biologists are

more backward than entomologists. In this day it is folly to rely, as we do, on catalogues often 50 years out-of-date and on the memories of a few specialists to keep track of 800,000 named insects. We know full well that this number represents less than half the actual total of the world's insect fauna. To this problem may be added the multitude of facts relative to the distribution, bionomics, and economic importance of each species. Thus, some measure of the magnitude of the task may be realized.

Basic to any efficient information storage and retrieval system is a means of associating related information according to fixed categories. We know that nature observes no fixed category boundaries, but we are not concerned with biological relationships, only with the practical problem of handling information. For this purpose we need a limited number of fixed categories arranged in a hierarchical order that will break up the accumulated information into manageable units.

No better master system has been devised than the commonly accepted hierarchy of taxonomic categories: Kingdom, Phylum, Class, Order, Family, Genus, Species. Of these categories the definition of only the species is reasonably objective. The only objective way to define taxa above the species is to say that each of these groups is composed of one or more units of the next lower category. It is true that each group should be separated by a gap, but unfortunately, these gaps come in all sizes and their importance is often best correlated with the resolving power of specialization. With a given specialist much depends on whether he looks for similarities or differences.

Since practical considerations demand that we have some fixed points of reference within the taxonomic hierarchy and because taxa above the genus are highly subjective in character, I can see no scientifically valid reason why the rank to be accorded groups placed in family, order, or higher categories should not be arbitrarily fixed. I do not mean that changes could not be made. But only that such changes should be made after evidence shows conclusively that a group contains elements that are less closely related to each other than one or more are related to elements of another group.

One guiding principle might be adopted that could eliminate most of the splitting of families and the elevating of subfamilies to family rank. The same principle could apply to orders, classes, and even phyla. The principle is as follows: no taxonomist should split, elevate, or demote supergeneric categories unless he has studied all coordinate groups and has integrated these units into his system of classification.

This principle implies that the taxonomist who wishes to elevate a subfamily to family rank would be obliged to work down from the superfamily, and preferably the suborder. Most taxonomists who propose new families work up through the hierarchy. They find groups of genera that they place in tribes. Groups of tribes form subfamilies. Of course, two or more subfamilies require recognition as a family. The size of the gaps separating the groups and the relative heterogeneity or homogeneity of the individual groups are of secondary importance. Actually the family rank is determined by the number of levels the taxonomist is able to find within the hierarchical arrangement of genera and supergeneric groups. The existence of gaps defining the different levels can and probably does have phylogenetic significance, but such a relationship can be shown in text rather than by a formal application of names. Or, if the taxonomist must have names, he should remember that the taxonomic hierarchy is indefinitely expandable within the limits of the family. After he has exhausted the subfamily, tribe, subtribe, division, and series taxa, he is free to invent additional levels.

Stabilization of familial and ordinal names would greatly facilitate mechanical handling of information about insects.

With the present uncertainty regarding the status of supergeneric names, codification of data for I.B.M. processing requires two digits for an order, and one for a suborder; two digits for a superfamily, three for a family, two for a subfamily; three for a genus; and three for a species. If the order and family were stable, digits for suborder, superfamily and subfamily could be dispensed with. Thus five digits would be saved for a more productive purpose than a hedge against the taxonomist's inability to decide whether a group is entitled to subfamily or family rank.

I believe that most taxonomists wish their work to be useful. But many think of usefulness in terms of three or four specialists who work in their same field. I believe that the specialist should think also in terms of the usefulness of his work to the non-specialists. Whether the taxonomist likes it or not, certain key steps in the taxonomic hierarchy have utility, and other biologists will judge taxonomists largely by how well their science serves as a vehicle for communicating information. Anything that contributes to the stability of familial and ordinal names contributes to this goal. At least the credit balance of any proposed change should always be compared with the debit that will result in the area of communication. As a general rule, the taxonomist should studiously avoid tinkering with familial or ordinal names unless he is prepared to overhaul the entire system of coordinate names.

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